

THE TAXONOMY, CYTOLOGY, AND EVOLUTION OF THE GENUS *RHAGOLETIS* IN NORTH AMERICA (DIPTERA, TEPHRITIDAE)

TABLE OF CONTENTS

	Page
Introduction	433
Acknowledgments and Sources of Material	434
Methods	435
Terminology	437
Biology of the Genus <i>Rhagoletis</i>	438
The Origin and Evolution of North American <i>Rhagoletis</i>	443
Genus <i>Rhagoletis</i> Loew	449
Key to North American Species of <i>Rhagoletis</i>	454
<i>Pomonella</i> Species Group	455
<i>R. pomonella</i> (Walsh)	457
<i>R. zephyria</i> Snow	464
<i>R. mendax</i> Curran	466
<i>R. cornivora</i> n. sp.	470
<i>Cingulata</i> Species Group	472
<i>R. cingulata</i> (Loew)	473
<i>R. indifferens</i> Curran	477
<i>R. osmanthi</i> n. sp.	478
<i>R. chionanthi</i> n. sp.	482
<i>Suavis</i> Species Group	482
<i>R. suavis</i> (Loew)	483
<i>R. completa</i> Cresson	488
<i>R. juglandis</i> Cresson	490
<i>R. boycei</i> Cresson	492
<i>R. zoqui</i> n. sp.	493
<i>Tabellaria</i> Species Group	495
<i>R. tabellaria</i> (Fitch)	495
<i>R. juniperina</i> Marcovitch	500
<i>R. persimilis</i> n. sp.	503
<i>R. ebbetsi</i> n. sp.	504
<i>Ribicola</i> Species Group	504
<i>R. ribicola</i> Doane	505
<i>R. berberis</i> Curran	509
Miscellaneous Species	510
<i>R. basiola</i> (Osten Sacken)	510
<i>R. striatella</i> van der Wulp	514
<i>R. fausta</i> (Osten Sacken)	518
Literature Cited	521

TABLES

	Page
1. The probable origin and current distribution of North American <i>Rhagoletis</i> species groups	443
2. Results of crosses between "host races" of <i>Rhagoletis</i> in the <i>pomonella</i> species group	456
3A. Body and wing measurements of males of the <i>pomonella</i> species group	459
3B. Body and wing measurements of females of the <i>pomonella</i> species group	459
4. Surstyli ratio and angle of the <i>pomonella</i> species group	460
5. Medial and subapical crossband width ratios of the wing for the <i>pomonella</i> species group	460
6. Members of the family Rosaceae recorded as hosts of <i>R. pomonella</i> ...	467
7. Species of Ericaceae found infested by <i>R. mendax</i>	468
8. Frequency of apical wing spot in the <i>cingulata</i> species group	474
9A. Body and wing measurements of males of the <i>cingulata</i> species group	475
9B. Body and wing measurements of females of the <i>cingulata</i> species group	475
10A. Body and wing measurements of males of the <i>suavis</i> species group ...	485
10B. Body and wing measurements of females of the <i>suavis</i> species group ...	485
11A. Body and wing measurements of males of the <i>tabellaria</i> species group	496
11B. Body and wing measurements of females of the <i>tabellaria</i> species group	496
12A. Body and wing measurements of males of the <i>ribicola</i> species group and miscellaneous species	506
12B. Body and wing measurements of females of the <i>ribicola</i> species group and miscellaneous species	506
13. Species of <i>Rosa</i> from which <i>R. basiola</i> has been reared	514

DISTRIBUTION MAPS

	Page
1. <i>Rhagoletis pomonella</i> (Walsh)	463
2. <i>Rhagoletis zephyria</i> Snow	465
3. <i>Rhagoletis mendax</i> Curran	469
4. <i>Rhagoletis cornivora</i> n. sp.	471
5. <i>Rhagoletis cingulata</i> (Loew), <i>R. indifferens</i> Curran	479
6. <i>Rhagoletis osmanthi</i> n. sp., <i>R. chionanthi</i> n. sp.	481
7. <i>Rhagoletis suavis</i> (Loew), <i>R. completa</i> Cresson, <i>R. juglandis</i> Cresson, <i>R. boycei</i> Cresson, <i>R. zoqui</i> n. sp.	487
8. <i>Rhagoletis tabellaria</i> (Fitch), <i>R. persimilis</i> n. sp., <i>R. ebbetsi</i> n. sp.	499
9. <i>Rhagoletis juniperina</i> Marcovitch	502
10. <i>Rhagoletis ribicola</i> Doane	508
11. <i>Rhagoletis berberis</i> Curran	511
12. <i>Rhagoletis basiola</i> (Osten Sacken)	515
13. <i>Rhagoletis striatella</i> van der Wulp	517
14. <i>Rhagoletis fausta</i> (Osten Sacken)	520

THE TAXONOMY, CYTOLOGY, AND EVOLUTION OF THE GENUS *RHAGOLETIS* IN NORTH AMERICA (DIPTERA, TEPHRITIDAE)

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INTRODUCTION

The genus *Rhagoletis* (tribe Trypetini, subfamily Trypetinae) was first proposed by Loew in 1862 to include only *Musca cerasi* Linnaeus and its synonyms. Therefore, *M. cerasi* is automatically the type of the genus by monotypy.

The generic limits of *Rhagoletis* have never been in doubt except for some disagreement over the status of a group of predominantly yellow Palearctic species sometimes placed in a separate genus, *Zonosema* Loew, and the recently established genera *Microrrhagoletis* Rohdendorf and *Megarrhagoletis* Rohdendorf. These are not recognized in the present revision. However, since controversy still exists over these genera, and questions have been raised in this revision about the relationships between *Rhagoletis* and the closely related genera *Carpomyia* A. Costa and *Zonosemata* Benjamin, an attempt has been made to present as detailed an analysis as possible of the generic limits of *Rhagoletis*. Examination of Palearctic and Neotropical material borrowed from the Museum of Comparative Zoology and the U.S. National Museum, and specimens exchanged with the Leningrad Zoological Institute have made it possible to establish the relation-

ships between various species groups with greater certainty.

The genus is widely distributed over the Holarctic and Neotropical regions and includes species that are major economic pests of fruits such as apples, cherries, walnuts, and tomatoes. Approximately 50 species and subspecies have been described, and the host plants are known for at least 42. Because of the economic importance of the genus, an extensive literature on the biology and control of certain species has accumulated over the past 100 years. One of the outstanding features emerging from these investigations is the frequent occurrence of morphologically almost indistinguishable, but apparently ecologically independent sympatric populations associated with different host plants. These populations have been variously regarded as host races, subspecies, and in some cases distinct species.

The presence of host races and sibling species in *Rhagoletis* and many other phytophagous insects has led some authors such as Brues (1924), Thorpe (1930), and Smith (1941), as well as others, to consider sympatric speciation as the most plausible explanation for the origin of many phytophagous insect species. Mayr (1963), on the other hand, contends that although host races may represent a possible case of incipient sympatric speciation, complete stabilization on a new host cannot occur without geographic isolation. However,

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conclusive evidence in support of these hypotheses is lacking. The problem, as pointed out by Mayr, cannot be satisfactorily resolved until adequate studies are undertaken to establish the degree of reproductive isolation between different host races of the same species coexisting in the same locality.

Much of this information is already available in the economic literature pertaining to insects associated with the food crops of man. Because most of these investigations were conducted before the biological species concept was widely accepted, systematists often dismissed the results as irrelevant to the taxonomic interpretation of host races and sibling species. This early work continues to be overlooked by modern taxonomists, but the results are no less important in the interpretation of host races today than they were in the early part of the century. Most taxonomists and economic entomologists of the Tephritidae, for example, have taken a purely morphological approach in their interpretation of the differences evident in allopatric and sympatric populations associated with different hosts. For example, Benjamin (1934) and Pickett (1937), with ample biological data at hand as a result of rearing and crossbreeding experiments, considered only morphological evidence in their interpretation of host races and sibling species. This typological approach has only confused rather than clarified the status of host races of *Rhagoletis* and many other phytophagous insects.

The objective of the present revision, therefore, has been to incorporate as much of this biological information as possible into a re-evaluation of these so-called host races. Additional observations made in three years of field and laboratory work on such aspects of the problem as chromosome cytology, courtship behavior, distribution, and host relations have also been included.

The interpretation which has emerged as a result of this investigation regarding host races in *Rhagoletis* is quite different

from that accepted in the past. Based on criteria established in this revision, most races appear to be distinct species and are probably oligophagous and not monophagous or polyphagous as once believed. Paleontological evidence of past plant distributions, as well as the present distribution of host plants, and of species of *Rhagoletis* currently associated with them, strongly supports allopatric speciation as a major source of new species. However, some sympatric sibling species may have become established through allochronic isolation on different hosts.

Certain aspects in the adaptation to new hosts, such as the genetics and chemistry of host selection, conditioning, and mating behavior, have yet to be studied. More thorough crossbreeding work and field studies on the ecology of this genus are badly needed. The hosts of several species are still unknown and the distribution of most species, including all those of economic importance, is yet to be definitely established.

The results presented here represent only a preliminary treatment of a very complex problem; consequently, the conclusions should be regarded as tentative. However, it is hoped that this study will furnish a basis for further investigations.

ACKNOWLEDGMENTS AND SOURCES OF MATERIAL

Although *Rhagoletis* is an economically important genus, it is poorly represented in most museum collections. However, through the cooperation of many individuals and institutions I have been able to amass a considerable number of specimens for study. I am deeply indebted to the following for making their collections available to me: Dr. S. Marcovitch; Prof. S. C. Jones; Academy of Natural Sciences of Philadelphia; American Museum of Natural History; California Department of Agriculture; Canadian National Collection; Carnegie Museum; Cornell University; Illinois Natural History Survey; Iowa State Uni-

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Additional material was collected during three summers of field work in the United States, Canada, and Mexico. These field trips were supported in part by a grant-in-aid of research from the Society of the Sigma Xi, fellowships from the National Science Foundation, and through the assistance of Harvard University. A number of individuals assisted me in locating material and in providing working facilities during the course of these field investigations. Space does not permit more than a mention of their names, but I wish to extend my sincere thanks to the following individuals: Dr. M. M. Barnes, Mr. F. L. Blanc, Mr. A. Forbes, Prof. S. C. Jones, Mr. P. Marucci, Mr. H. R. Moffitt, Mr. A. D. Pickett, Dr. M. Wasbauer, Dr. F. Werner; and members of the staff of the U.S. Department of Agriculture Fruit Fly Laboratory, Mexico City: Mr. W. Stone, Dr. F. Lopez-D., Sr. L. Torres-N., Sr. V. Torres-N., and Sr. F. E. Guiza.

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METHODS

Morphology. In order to facilitate identification of various structures referred to in the text, illustrations of the most important diagnostic characters are presented in Figures 1-16. The terminology follows that of Dean (1933, 1935), Munro (1947), and Steyskal (1957).

Chromosome morphology. The terminology in the description of chromosome morphology is that of White (1957), and Bush (1962). MCA refers to the number of major chromosome arms. Gonads and larval brain tissue were prepared for study following the method I described in 1962.

Description of color. General terms have been used to describe variation in color. Whenever possible the terminology is based on the standardized color names of the *Dictionary of Color* (Maerz and Paul, 1950). The following is a list of the color names used in the text and the code used

to designate the color in the *Dictionary of Color* which may be referred to if a more accurate interpretation is needed. Golden yellow, 9I5; tannish cream, 9E3; dark yellowish orange, 9L8 and 9L10; light yellowish orange, 9L4 and 9L5; yellowish orange, 9L7; brown, 7E10; lemon yellow, 9K3; tawny, 13D10; light brown, 13L10; yellowish cream, 9G2; golden tan, 10L7; golden brown, 12I8; tan, 12L10; reddish brown, 4D12.

Abbreviations used in the text. The following abbreviations are used in the lists of synonymy: ANSP (Academy of Natural Sciences of Philadelphia); AMNH (American Museum of Natural History); CNC (Canadian National Collection); CU (Cornell University); KU (Kansas University); LZI (Leningrad Zoological Institute); MCZ (Museum of Comparative Zoology); USNM (United States National Museum); GLB (Guy L. Bush).

Authorities for the botanical names are abbreviated following the form employed in the eighth edition of *Gray's Manual of Botany* by M. L. Fernald (American Book Company, New York) in the section entitled "Explanation of Abbreviated Names of Authors," pp. liii–lviii.

Locality and host data accompanying specimens. The large number of specimens examined, particularly in certain species of economic importance, has made it necessary to exclude detailed information appearing on the specimen labels.² Data of this nature have been summarized in distribution maps of individual species in relation to their respective hosts, and a brief résumé of pertinent features of the distribution accompanies the discussion of each species.

Lists of synonymy and other pertinent references. As previously mentioned, a great deal of literature has accumulated on certain economic and biological aspects of this genus. An attempt has been made to review all of this material except for a few strictly economic papers. Only the pertinent literature has been referred to in this revision, and the lists of synonymy have been kept as short as possible.²

Measurements. Certain species can only be distinguished on the basis of body measurements and indices; therefore, these must be made with accuracy. Measurements were always made by rotating the specimen until the maximum measurement was obtained. This reduced the error in measurement to a minimum by insuring that the distance between the two points being measured was at right angles to the line of vision (see Brown, 1953). All body and head measurements were made at 100× using an ocular micrometer. Wing measurements were made from slide mounted wings using a Bioscope. Structures such as the abdomen and ovipositor sheath were found to be of little use as they were distorted greatly by desiccation, thus making it impossible to obtain accurate measurements.

Measurements were made in the following way: HL—head length—measured in profile from base of antennae to base of comb; HW—head width—maximum width measured in frontal view; HH—head height—measured in profile from lower margin of genae to vertex; EW—eye width—maximum width measured in fronto-lateral view so that both lateral margins are in focus; EH—eye height—maximum height measured in a slightly dorsal and fronto-lateral view so that both upper and lower eye margins are visible; FrWV—frons width at vertex—the maximum distance between the margin of each eye measured in dorsal view along the anterior edge of the ocellar plate; AL—antennal length—measured in frontal view from upper margin of 1st segment to tip of 3rd segment; FL—face length—measured in frontal view from the peak

² For those interested in detailed distribution data and in an annotated list of references, the author's Ph.D. thesis, "A revision of the genus *Rhagoletis* in North America (Tephritidae, Diptera)," may be obtained on loan from the librarian of the Biological Laboratories, Harvard University. Mimeographed copies of this information have also been placed in the libraries of the Museum of Comparative Zoology and the United States National Museum.

of the ptinial sulcus to the lower margin of the face; GW—genal width—difficult to measure accurately as the shape of the genae varies among individuals; best taken as the maximum length between the lowermost corner of the eye and the lower margin of the gena just in front of the genal bristle; TL—thorax length—maximum length measured in dorsal view from the tip of scutellum to the most anterior region of pronotum; WL—wing length—maximum distance between small break or cross sulcus in base of radial sector located just basad of junction of radial sector and humeral crossvein to end of R_{4+5} ; WW—wing width—maximum width measured apicad of subcostal break.

Identification of host plants. Most of the hosts of the more common species of *Rhagoletis* were easily recognized in the field, though some could only be identified to genus. In doubtful cases, specimens were pressed and returned to the laboratory for study. Those specimens that could not be identified to species with certainty were deposited in the Gray Herbarium of Harvard University where future workers interested in host relationships may obtain an identification if specialists can be located.

Rearing. Infested fruit was placed over moist sand until all larvae had left the fruit and pupated. After two weeks the pupae, in some moist sand, were refrigerated at 4° C for two to three months. They were then removed and the sand moistened again. Usually adults began emerging within 25 to 30 days. Attempts were made to maintain the adults on a variety of diets, but the only one that proved successful consisted of powdered milk, bakers yeast, and sucrose fed in dry form. Flies had access to water at all times. Adults were permitted to live at least four days before they were pinned to insure maximum coloration and internal development.

TERMINOLOGY

Monophagy, oligophagy, and polyphagy. The use of the terms monophagous, oligophagous, and polyphagous presents special problems of interpretation. Thorsteinson (1960) maintains that a classification of food preferences in purely chemotactic terms is preferable to the more subjective system based on the number of plant species infested by an insect. While recognizing the importance of chemical stimuli in host plant selection, it is still impractical to apply this method in a discussion of host relationships in *Rhagoletis* because the chemical basis for host selection is not known. The interpretations given below have been followed in this revision.

A monophagous insect is restricted to a single species of host plant while an oligophagous insect utilizes several host species within the same genus or related genera of plants of the same family. A polyphagous species infests a wide range of host plants in several unrelated host genera of different families.

Host races and sibling species. *Host races* are morphologically similar or indistinguishable populations of an ecologically polymorphic species, each of which is restricted to a single host or a group of closely related hosts. As races they are not reproductively isolated from one another and gene flow can be re-established between them when ecological or geographical barriers are removed. This is in contrast to *sibling species* which have been defined by Mayr (1963) as morphologically similar or identical populations which are reproductively isolated.

In the absence of sufficient biological data, it is difficult or impossible to establish whether two or more morphologically closely related populations represent distinct sibling species or simply host races. The following "rule of thumb" was therefore used in handling this problem during the course of the present revision.

Two closely related sympatric populations associated with different host plants

and showing slight but consistent morphological differences were considered sibling species if the host plants belonged to different families or even distinct genera within a family.

The use of the host family as a criterion for establishing the status of most host races and sibling species in cases where reproductive isolation in *Rhagoletis* cannot be established seems justified on the basis of crossbreeding work conducted on members of the *pomonella* group. In this species group certain populations formerly considered only host races associated with different plant families, such as Rosaceae, Cornaceae, Caprifoliaceae, and Ericaceae, have all proved to be distinct species. Populations in the *pomonella* group associated with closely related genera within a family, however, are capable of interbreeding at least under laboratory conditions (cf. p. 455).

Morphologically distinct allopatric populations infesting either related or unrelated host plants were considered distinct species if the morphological differences between them were as great as or greater than the differences encountered between sympatric species within the same species group.

If no morphological differences could be correlated with host preference in allopatric or sympatric populations, and if the biology of the species was not well known, then the various populations associated with different hosts were considered host races.

Sympatry (Mayr, 1963). The occurrence of two or more populations in the same area. Mayr has limited this term to a population in breeding condition within cruising range of individuals of another population.

Sympatric speciation (Mayr, 1963). Speciation without geographic isolation; the acquisition of isolating mechanisms within a deme.

Allopatry (Mayr, 1963). The occurrence of populations or species occupying mu-

tually exclusive (but usually adjacent) geographical areas.

Allopatric speciation. Speciation with geographic isolation; the acquisition of isolating mechanisms in two or more geographically isolated populations of the same species.

Syntrophic. Sharing the same or closely related food source.

Allotrophic. Utilizing different food sources.

Allochrony. The occurrence of conspecific populations or species in breeding condition (e.g., host races) at different times of the year.

Allochronic speciation. Speciation by temporal isolation. The acquisition of isolating mechanisms in two or more allochronically isolated populations.

BIOLOGY OF THE GENUS *RHAGOLETIS*

A complete review of the biology of *Rhagoletis* will not be attempted here. Reference may be made to Illingworth (1912), O'Kane (1914), Porter (1928), Nicholson (1929-30), Lathrop and Nickels (1932), Boyce (1934), Pickett (1937), Wiesmann (1937), and Christenson and Foote (1960) for further details. A few salient features of the biology should be mentioned, however, as they not only have a direct bearing on the population structure and evolution of the flies themselves, but also offer clues that may be used to interpret the status of the many host races recorded in this genus.

Larval food habits. As far as is known, the larvae of all species feed in the fleshy pulp of fruits and berries. Based on the criteria used in this revision to denote the degree of host specificity, all species are probably oligophagous, being restricted to a narrow range of closely related hosts. None that have been carefully studied were found to be either monophagous or polyphagous as previously reported by some authors. Although oligophagous, most species show a definite preference for certain host species within a genus, or even for

particular varieties of a single species (Illingworth, 1912; O'Kane, 1914; Wellhouse, 1920; Lathrop and Nickels, 1932).

Host transfer experiments. Most of the sibling species formerly considered host races show some minor morphological differences, particularly in overall size and in the structure of the genitalia. Some authors have attributed these differences either to nutritional qualities of the various hosts or to geographic variation (Benjamin, 1934; Pickett, 1937; Hall, 1938). Host transfer experiments conducted by several investigators indicate that genetic factors may also be involved. Lathrop and Nickels (1932) found that first and second instar larvae of *R. mendax* from blueberries would complete development when placed in apples, but the resulting pupae and adults were of the normal small size typical of the blueberry form. When *R. pomonella* from apples was transferred to blueberries, or induced to oviposit in this fruit, the resulting pupae and adults were of normal size for the apple form. This would indicate that in these two reciprocal host transfers the genotype and not the food supply determined body size.

Nutrition and crowding seem to influence adult size in some instances. Hall (1938) reported that pupae and adults resulting from the forced oviposition by *R. pomonella* in *Cornus* berries were smaller than normal, suggesting a nutritional effect on body size. It does not follow, however, that the sibling species, *R. cornivora*, which infests *Cornus*, is smaller because of a nutritional deficiency in its host fruit. Reciprocal infestation of *R. cornivora* in apples was not made, as the adults refused to oviposit in the fruit. The small size of both *cornivora* and *mendax* undoubtedly has some adaptive function that has not been determined as yet.

In the *suavis* group where many females may oviposit on a single walnut, crowded conditions may result in abnormally small adults (see *Hosts*, *R. completa*). In other species groups, more than one larva in a

fruit is rare (except in the case of infestations in large fruits such as apples). Multiple oviposition in these species is apparently inhibited by a pheromone laid down by the female prior to oviposition (Hafliger, 1953).

Diapause and emergence. All Holarctic species of *Rhagoletis* that have been studied are essentially univoltine, with the adults of various species emerging at different times during the summer. Usually, diapause must be broken by a period of low temperature, some individuals requiring as many as four successive chillings in as many years before they complete development (Boyce, 1934). At least one Neotropical species, *R. lycopersella* Smyth which infests tomatoes in Peru, apparently is adapted to arid conditions. Its diapause can be terminated by simply placing pupae in a moist environment (Smyth, 1960). These characteristics are of considerable selective advantage as they insure a supply of adults every year even though the host in a given area fails to bear fruit for several consecutive seasons.

Emergence generally occurs over a relatively short period with 60–90 per cent of the flies emerging within two to four weeks. This emergence is synchronized with the maturation of the host fruit and usually never varies more than two weeks from year to year. A few flies, however, emerge up to a month before and after the peak emergence period. These early and late emerging flies are at a considerable selective disadvantage, and a substantial number probably perish without leaving progeny since host fruits are not readily available for oviposition. They do, however, insure the presence of some flies to maintain a resident population in years when for some reason peak emergence does not coincide with host maturation. The rare occurrence of such an event in any one area possibly accounts for the low frequency of these "off season" flies in natural populations. They may also play an important role in the

formation of new host races and species through allochronic speciation (p. 447).

The factors controlling diapause in the North American and European species are not well understood. The close adaptation of various species to the fruiting times of their respective hosts would indicate that emergence periodicity is under genetic control and is probably regulated by certain components of the environment, such as temperature and day length.

Illingworth (1912), Hall (1938), and others have noted a small second brood in *R. pomonella*. A few adults may emerge late in the summer or early fall from larvae that pupated the same year. Hall (1938) observed that second brood adults emerging in the same summer in which they pupated were obtained in Ontario only from pupae formed before August 20. This suggests that light (day length), temperature, or both, may influence emergence by acting in some way on the host plant or on the previous generation of flies. Diapause may, therefore, be facultative and not obligatory, at least in some individuals.

Normally these flies would find few fruits in which to oviposit, and it is unlikely that their larvae, if any are produced, could complete development before freezing temperatures set in. A second brood may be important in the southernmost part of the range of certain species of *Rhagoletis* where host maturation is spread over a longer period and where freezing temperatures occur infrequently. But in these areas there is no indication as yet of a regular second brood.

Adult longevity. Adults are known to live up to 70 days in the laboratory, but it is doubtful that many ovipositing females survive for more than 20-30 days under natural conditions.

Flight range and dispersal. Recent investigations using radioactively-labeled flies demonstrated that *R. completa* is capable of dispersing up to one mile in 21 days and probably farther under favorable conditions (Barnes, 1959). Studies on other Tephriti-

dae, such as *Dacus dorsalis* Hendel, *Ceratitis capitata* (Wiedemann), and *Anastrepha ludens* (Loew), indicate that these flies are capable of covering considerable distances over unfavorable areas (Christenson and Foote, 1960). *A. ludens*, for instance, is known to travel 160-175 miles from the nearest breeding areas in northern Mexico to southern Texas. Prevailing winds are apparently the most active agents in dispersal. Distance and unfavorable terrain, therefore, cannot always be considered absolute barriers to dispersal. Normally, however, adults of *Rhagoletis* do not disperse rapidly if suitable hosts are available, but congregate in trees which bear fruit in suitable condition for oviposition.

Mating behavior and territoriality. Courtship in most species of *Rhagoletis* that have been observed relies heavily on visual cues. Males court and females respond to courtship with various movements of the wings and body which are adorned in both sexes with contrasting color patterns. Use of the wings in courtship displays may account for the widespread occurrence of distinctive species specific and occasionally sexually dimorphic wing patterns in many groups of Tephritidae.

Sexual dimorphism in color pattern of the body is found in two widely separated *Rhagoletis* species groups. Three of five species in the *suavis* group show varying degrees of differences in thorax and abdomen coloration, the males being much more heavily pigmented with black than the females. In the *ribicola* group, the legs of *R. ribicola* males are entirely yellow. Only the front pair of legs in the female are yellow, while the other two pairs are dark brown. These patterns apparently play a role in sex and species recognition.

The fact that males of *R. completa* respond to certain chemical lures (Barnes and Osborn, 1958) also suggests that chemical releasers play some as yet undetermined role in courtship. Pheromones are known to be used as sex attractants by females of some species of Tephritidae (Christenson

and Foote, 1960), and Féron (1962) has shown that, at least over short distances, males of *Ceratitis capitata* also produce a sex attractant during the initial stages of courtship. It would not be surprising to find similar pheromones in other tephritids as well.

However, both sexes of many species of *Rhagoletis*, *Anastrepha*, and other tephritid genera respond to certain fermenting and chemical lures (Christenson and Foote, 1960). These apparently do not simulate sex pheromones, but seem to mimic odors produced by either a suitable food supply or oviposition site. This suggests that certain odors emitted by host plants may function as secondary sex attractants since they bring the two sexes together on a common host or food source. This is apparently the case in *Rhagoletis* and many other tephritids where mating occurs on or near the host plant. Plant odors may therefore be particularly important as a rendezvous stimulus in those groups of Tephritidae that rely primarily on visual releasers in courtship in the absence of long distance chemical or auditory unisexual sex attractants.

Auditory releasers commonly used in courtship by species of *Dacus* (Monro, 1953; Browne, 1957b) and *Ceratitis* (Féron, 1960) have not been demonstrated in any species of *Rhagoletis*. However, there is some indication that light intensity influences courtship as it does in *Dacus tryoni* (Froggatt) (Browne, 1957a) and *Ceratitis capitata* (Féron, 1957). In *R. completa*, courtship and mating are most frequently observed in the late afternoon (Boyce, 1934).

The fact that courtship and mating occur on the host plant means that there is little chance for sympatric allotrophic populations of host races and sibling species to encounter one another during this critical phase in their life cycle. Therefore, the restriction of mating to the host plant has important implications in the formation of host races and speciation.

Males of the *suavis* group are known to

be territorial, and there is good evidence to suggest that the other species of *Rhagoletis* also maintain temporary or "floating" territories consisting of a single fruit or a cluster of fruits.

Host specificity and oviposition behavior. Evidence has been presented which indicates that under both laboratory and field conditions many species of *Rhagoletis* are capable of ovipositing in a wide range of fruits which are not their normal hosts. In some cases, mature larvae and even adults of a particular species have been reared in the laboratory from hosts that are never found infested by the species in the field. For example, Pickett (1937), and Pickett and Neary (1940) were able to induce *R. pomonella*, a species infesting several genera of Rosaceae (Table 6), such as haw (*Crataegus*), apple (*Pyrus*), and plum (*Prunus*), to oviposit in such fruits as blueberry (Ericaceae) and snowberry (Caprifoliaceae). Other genera in the Rosaceae that are not normally considered hosts, i.e., pear (*Pyrus*), mountain ash (*Sorbus*), and sweet cherry (*Prunus*), were also artificially infested by *pomonella*. In addition to these oviposition records, Hall (1938) was able to induce *pomonella* to oviposit in tomato (Solanaceae) and *Cornus amomum* (Cornaceae). Mature larvae developed in all these fruits, but the number recovered was usually abnormally low. With the exception of pear and mountain ash, all of these plants are hosts for other species of *Rhagoletis*, some very closely related to *pomonella*.

Even under natural conditions, these flies are not host specific in their oviposition habits. Glasgow (1933) found that *pomonella*, *cornivora*,³ *tabellaria*, *cingulata*, and *fausta* regularly oviposited in the fruits of 30 out of 39 species of fruit-bearing plants growing in the vicinity of infested apple and cherry trees. Of these 30, only 15 served as normal hosts while the remaining

³ Glasgow did not recognize *R. cornivora*, but considered the *Cornus*-infesting form to be *R. pomonella*.

15 were apparently unsuitable for larval development. Although eggs and larvae were frequently found in these non-host fruits, adults were never reared. Glasgow concluded that the *Rhagoletis* under study were somewhat lacking in discrimination in their egg laying habits, and undoubtedly oviposited in many fruits in which there was no possibility of the species surviving.

But indiscriminate oviposition may not be the whole answer. Often the female will pierce the fruit of both host and non-host species with her ovipositor but deposit no eggs. Instead, she will turn and feed on the exuding fruit juice. Even when eggs are deposited, the female may often feed in a similar manner (Doane, 1898; Boyce, 1934; Tominic, 1954). Oviposition and pseudo-oviposition (when eggs are not deposited) in some cases may therefore function as a means of acquiring necessary nutrients.

The non-host fruits involved in pseudo-oviposition are also not as indiscriminately selected as Glasgow assumed. Of the 15 species of non-host plants in which oviposition occurred, 13 belong to genera, and sometimes even represent the same species, infested by other *Rhagoletis* species. There may be some component of the plant or fruit which either mimics the normal host plant or furnishes something needed by the female in her diet. The habit of selectively ovipositing in what are normally non-host species may also account for the fact that species of *Rhagoletis* from widely separated groups have independently become adapted to the same genera and sometimes the same species of plants. If a fortuitous mutation or recombination permits larvae to survive in the new host, a new host race may eventually become established.

To my knowledge, the genetics of host selection and the ability to survive in any given host has not been established for any species of phytophagous insect. The ability of many tephritids to rapidly establish host races on introduced plants, however, would indicate that only minor shifts in the genotype are required in some cases.

Distribution of Rhagoletis in relation to host plants. It might be expected that by now the distribution of such economic pests as *R. pomonella*, *R. cingulata*, and *R. completa* would be fairly well established, but unfortunately this is not the case. However, enough is known to indicate that most, if not all, species do not cover the entire range of their hosts. Although the various species are ultimately dependent on their host plants, other factors seem to restrict their distribution. Thus, in many cases host plants may be continuous over most of North America, but the *Rhagoletis* associated with them can be found only in certain parts of the host range.

With the exception of the *suavis* group and possibly several Neotropical species, all other *Rhagoletis* species are restricted to fairly temperate mesic conditions with substantial rainfall and seasonal change. None of the northeastern species of *Rhagoletis* whose hosts extend more or less continuously over northern United States and southern Canada, are able to penetrate much beyond the 100th meridian. Even those species of the *suavis* group found in semi-arid regions of Mexico and southwestern United States are associated with walnuts growing in moist conditions along stream beds or at high altitudes. Most species, therefore, appear to be less tolerant than their hosts of dry conditions. This factor has probably played a major role in limiting the distribution of many species. Slight climatic changes could leave isolated pockets of flies even though the distribution of the host remained more or less continuous. These populations of flies, if isolated for a sufficient period, could be a source of new species and could have some influence on the evolution of a temperate climate genus such as *Rhagoletis*.

Geographical variation. Two morphological trends associated with latitude have been noted in several *Rhagoletis* species. There is a tendency toward an overall reduction in size at the more southern limits of the range of such wide-ranging species as *pomonella*, *completa*, and *cingulata*. A sec-

TABLE 1. THE PROBABLE ORIGIN AND CURRENT DISTRIBUTION OF NORTH AMERICAN *Rhagoletis* SPECIES GROUPS. HOST FAMILIES INDICATED IN PARENTHESES.

NORTH AMERICAN ORIGIN		EURASIAN ORIGIN OR WITH EURASIAN AFFINITIES		CENTRAL OR SOUTH AMERICAN ORIGIN	ORIGIN UNCERTAIN
East	N West	East	N West	East, S West and Mexico	N East and N West
POMONELLA GROUP		TABELLARIA GROUP		SUAVIS GROUP	
<i>pomonella</i> (Rosaceae)	<i>zephyria</i> (Caprifoliaceae)	<i>juniperina</i> (Cupressaceae)	<i>juniperina</i> (Cupressaceae)	<i>suavis</i> (Juglandaceae)	<i>fausta</i> (Rosaceae)
<i>mendax</i> (Ericaceae)		<i>tabellaria</i> (Cornaceae)	<i>tabellaria</i> (Ericaceae)	<i>completa</i> (Juglandaceae)	
<i>cornicora</i> (Cornaceae)			<i>persimilis</i> (host ?)	<i>juglandis</i> (Juglandaceae)	
			<i>ebbettsi</i> (host ?)	<i>boycei</i> (Juglandaceae)	
				<i>zoqui</i> (Juglandaceae)	
CINGULATA GROUP		RIBICOLA GROUP		STRIATELLA GROUP	
<i>cingulata</i> (Rosaceae)	<i>indifferens</i> (Rosaceae)		<i>ribicola</i> (Saxifragaceae)	<i>striatella</i> (Solanaceae)	
<i>osmanthi</i> (Oleaceae)			<i>berberis</i> (Berberidaceae)		
<i>chionanthi</i> (Oleaceae)					
ALTERNATA GROUP					
		<i>basiola</i> (Rosaceae)	<i>basiola</i> (Rosaceae)		

ond trend also found in these southern populations is a reduction in the extent of dark brown and black pigmentation. This is particularly apparent in *cingulata*. The reasons for these trends are not known.

THE ORIGIN AND EVOLUTION OF NORTH AMERICAN RHAGOLETIS

Geographical aspects of intrageneric relationships. The predominantly Palearctic *alternata* species group and also most of the Neotropical species show several close morphological affinities which may be considered primitive. They have the wing vein

R₄₊₅ setulose, and have retained the same basic wing pattern and head shape. The present disjunct distribution of species bearing these features, as well as the presence of these characters in other closely related genera such as *Zonosemata*, *Carpomyia*, and *Rhagoletoides*, suggest that they were present in the early stages of development of *Rhagoletis*. Although similar in these basic characters, the *alternata* group and Neotropical species have diverged considerably in other features, such as the shape of the spermathecae, and in their host relationships.

The more specialized members of the genus are concentrated in eastern North America and the Palearctic region, particularly in eastern Asia. Species from these regions bear few or no setae on R_{4+5} , and show a considerable variation in wing pattern and, to some extent, in head shape. As shown in Table 1, most of the North American representatives of the genus have originated from these two centers of secondary radiation which were probably established after the original dispersal of *Rhagoletis*.

Although the Neotropics has been a major center in the development of new species, it has furnished only *R. striatella* and possibly members of the *suavis* group to the North American region. Only one of these, *R. suavis*, has been able to reach the eastern part of the United States, and none has penetrated into the Northwest, which has been floristically cut off from Mexico since the Middle Pliocene (Axelrod, 1958). Since no members of the *suavis* group occur in native California species of walnuts but are found in Arizona and New Mexico, it is likely that this species group either did not become established on walnuts or did not reach Mexico and the Southwest until at least after the early Pliocene.

Historical aspects. The time and place of origin of the genus *Rhagoletis* are not known. The fact that most of the species are adapted to high altitudes or a temperate climate supports the Holarctic region as the most probable original center of radiation. There is no fossil record of any Tephritidae,⁴ although fossils of the closely related family Otitidae have been described from the Miocene Florissant shales of Colorado (Cockerell, 1915, 1916, 1917; Melander, 1949), and appear in the Oligocene Baltic amber (Loew, 1864). It is possible that tephritid representatives existed during or

before this time, but the large number of species in this family which infest the heads of composites, most belonging to the subfamily Tephritinae, could not have arisen much before the Miocene. Fossil pollen representing the earliest record of the large diversified plant family, Compositae, is not known before the lower Miocene (MacGinitie, 1958). The fruit-infesting forms could have arisen considerably earlier, as fossils of genera now infested by *Rhagoletis*, for instance, are frequently found in Cretaceous deposits.

As far as I have been able to ascertain, however, acalyptrates have never been described from the Cretaceous, and do not appear until the Eocene. Furthermore, evidence provided by the past floristic history of the Holarctic region and the present distribution of *Rhagoletis* indicates that the genus, as well as most other tephritid genera, arose sometime in the Oligocene or early Miocene.

It is now well established that a continuous temperate climate flora, usually referred to as the Arcto-Tertiary geoflora, existed until the late Eocene over the entire Holarctic region (Chaney, 1947; Axelrod, 1958). The northern elements of this flora were coextensive from Eurasia to western and, in some cases, eastern North America until the late Pliocene or Pleistocene break in the Bering land bridge. For some of the more southerly members of the flora, a climatic barrier has probably existed since Miocene times (Chaney, 1947).

Although this Miocene break may have occurred after the Tephritidae became established, it has apparently influenced the distribution of at least one subfamily.⁵ The Dacinae, whose members infest the fruits of various tropical and subtropical plants, probably originated during or after the Miocene break as it is presently widely represented in the Old World tropics and

⁴ Cockerell (1924) erroneously placed his *Eophlebomyia claripennis* from the Green River Eocene shales of Colorado in the family Tephritidae. This has since proved to be more closely related to the *Glossina*, and is definitely not an acalyptrate (Cockerell, 1925).

⁵ The distribution of the related family, Richardiidae (superfamily Tephritoidea, see Steyskal, 1961), which is restricted to tropical and subtropical America, indicates that this family also may have arisen after the Miocene break.

Australia but has only one highly specialized and aberrant genus, *Toxotrypana* Gerstaecker, in the New World.

Rhagoletis and other temperate climate genera, on the other hand, probably followed their host plants across the Bering land bridge whenever conditions were favorable during the late Tertiary and certain parts of the Quaternary. One host plant of *Rhagoletis*, *Rosa acicularis* Lindl., is still coextensive over Eurasia and North America (Lewis, 1959), and is infested by the Palearctic and Nearctic sibling species, *R. alternata* and *R. basiola*. In western North America, other hosts of *Rhagoletis*, such as *Mahonia*, *Juniperus*, *Ribes*, and *Vaccinium* of the subgenus *Euvaccinium*, have very closely related species or conspecific representatives in Eurasia or eastern Asia. All of these genera are infested by *Rhagoletis* belonging to Eurasian-centered species groups which probably entered western North America in the late Pliocene or Pleistocene.

Floristic connections between eastern and western North America, and between the West and Mexico, however, have not been continuous throughout the Cenozoic. Climatic changes initiated in the Lower Eocene established a barrier which by the Oligocene prevented the migration of floristic elements either southward into Mexico or eastward. This barrier existed well into the Miocene, during which time there was little exchange of plant species from the East to the Northwest, or between the West and Mexico.

Contact was evidently re-established between the East and West in the Upper Miocene, probably through southern Canada (MacGinitie, 1958). During the Upper Miocene, and possibly the early Pliocene, there was also some floristic interchange between Mexico and western North America, but apparently arid conditions prevailing in what is now Texas prevented a free interchange of species between Mexico and eastern North America (Dressler, 1954). It was probably during this time that *Rhago-*

letis penetrated southward into South America via a route through western North America.

Although land connections between North and South America were not established until the late Pliocene or early Pleistocene (Lloyd, 1963), hosts of *Rhagoletis*, such as *Juglans* and many of the solanaceous plants, were probably available for colonization long before continental connections were established. Considering the known ability of the Tephritidae to cover long distances over inhospitable terrain and water gaps, it is very likely that the many islands between Central and South America present during parts of the Cenozoic offered suitable steppingstones for dispersal.

Contact between the floras of Mexico and the West, and between the East and the West, did not exist for long as the cooling and drying trend that characterized the late Cenozoic soon replaced the subtropical scrub of the central plains area with the modern herbaceous vegetation. In the Northwest the cool dry climate of the Pliocene forced the Arcto-Tertiary geoflora both coastward and farther southward. This resulted in a disjunct east-west distribution in some genera. The dry summer climate of this period in North America also led to the disappearance from the West of a great many broad-leaf deciduous genera, including *Juglans*, which survived in eastern North America.

It is possible that some of the present sibling species pairs such as *R. pomonella*-*R. zephyria*, and *R. cingulata*-*R. indifferens* were established during this period of the Pliocene, although a later date is more likely. There was ample opportunity during the interglacial periods of the Pleistocene for such hosts as *Prunus*, *Cornus*, *Symphoricarpos*, *Crataegus*, and *Vaccinium* to re-establish contact through southern Canada and northern United States as they have done since the last glaciation. The Pliocene was, therefore, probably a time of extinction rather than generation

for many *Rhagoletis* species in the Northwest as their host plants disappeared.

This period also probably marks the time when the originally widespread *Rhagoletis* fauna was broken into at least three major groups, one in Asia, another in eastern North America, and a third in Central and South America. The present distribution of *Rhagoletis* supports this conclusion. A comparison of the native northwestern species with those of Eurasia and eastern North America (Table 1) shows that this region has no autochthonous species groups. All of its species have been either derived from the East or from Eurasia. Nor are there any known autochthonous sibling species in this region, a feature common to the Eurasian and northeastern species of *Rhagoletis*. Some of the species are, however, members of allopatric sibling species pairs with the other member of the pair in Eurasia or the Northeast.

Major physiographic and climatic changes in the late Pliocene and Pleistocene brought about a new reshuffling of the floristic elements between the East and West, and for the first time between the East and Mexico. During this period few, if any, connections were established between Mexico and the West. This was a time when much of the Rocky Mountain chain of western North America and the Sierra Madre Oriental of eastern Mexico were uplifted, and when four successive waves of glaciation caused repeated drastic shifts of the temperate flora (Dressler, 1954; Flint, 1957). When floristic connections between Mexico and eastern North America were established during the pluvial periods of glaciation, certain mesophytic and xeromesophytic representatives of the eastern temperate forest probably entered Mexico through the Big Bend region of Texas. Once in Mexico, they were able to survive in the newly formed mountains during the warm, dry interglacial periods (Dressler, 1954; Sharp, 1953). While floristic connections existed between Mexico and the East, *R. pomonella*, belonging to a group

centered in the East, probably penetrated into Mexico along with or following its host plant *Crataegus*. *R. suavis* and *R. completa*, both members of a predominantly Mexican-centered group, apparently also entered the East at this time either with *J. nigra* or when connections were established between Mexican *Juglans* and *J. cinerea* through expansion of their ranges.

The southeastern part of the United States also underwent drastic changes. The accumulation of the earth's water in the form of ice during glacial periods resulted in a drop in sea level exposing much of the now submerged gulf coastal plain. The interglacial periods, some of which were warmer and apparently drier than the present, brought about a subsequent rise in sea level which inundated the gulf coastal plain and left parts of Florida exposed as islands or small island archipelagoes. Presently associated with these former islands in Florida are many species and distinct races of plants and animals that had their origin as isolated populations during these interglacial periods (for summary see McCrone, 1963, and Howden, 1963).

Some of the species of *Rhagoletis* now restricted to the Southeast probably had their origin on these islands during the Pleistocene. The hosts of *R. osmanthi* and *R. chionanthi*, for example, are among the plants which have distinct subspecies presently associated with these former islands and offer an explanation for the apparently recent origin of these two sibling species of *Rhagoletis* in the Southeast.

Some of the southeastern as well as northeastern plants, such as *Osmanthus americanus*, *Cornus florida*, *Vaccinium arboreum*, and *Prunus serotina*, also have isolated populations in Mexico which are not known to be infested by any species of *Rhagoletis* associated with these plants in the East. If a careful search fails to locate these eastern species in the potential Mexican host populations, it will lend fur-

ther support for a recent origin of many eastern species of *Rhagoletis*.

Speciation in the genus Rhagoletis. Allopatric speciation is probably the most common pattern of evolution in *Rhagoletis* and may result in two quite distinct end products, depending on the initial degree of host specificity (or ecological amplitude) of the parent species.

The first involves divergence of two isolated populations of a species on the same or closely related host. This is best illustrated in the *suavis* group whose species normally infest only walnuts (*Juglans* spp.). Evidence of the past movements of *Juglans* (McVaugh, 1952; Manning, 1957) indicates that there was ample opportunity prior to and during the Pleistocene for allopatric speciation on isolated populations of walnuts. If contact between these populations was re-established through expansion of the range of their host plants or chance long distance dispersal, competition on the same host would be intense and, since mating in this genus occurs on the host plant, the chances for hybridization would be high. If there had been sufficient divergence in isolation, selection would favor adaptations increasing the frequency of homogamic matings.

Characters associated with visual releasers, which are important components of courtship displays and species recognition in this genus, have been exploited by the *suavis* group in the course of establishing isolating mechanisms. Each species has a distinctive wing pattern and body coloration, and three of the five species in the group show varying degrees of sexual dimorphism. Other adaptations, such as altitudinal preference and difference in emergence times, have also helped to reduce interspecific competition (see *Hosts* of *R. boycei*).

Geographic isolation in other species groups, however, has involved a shift to an entirely new host without a corresponding shift in characters associated with courtship behavior. Courtship and mating

in these groups would occur on different hosts, thus reducing the chance of hybridization. Competition for oviposition sites would, therefore, be negligible, and as a result, the need for the development of isolating mechanisms associated with visual releasers would be greatly reduced. Perhaps for this reason sibling species are found only in those groups whose members have widely different host preferences.

A shift to a new host could come about in two ways. A species with both primary and secondary hosts may become isolated on the secondary host in a locality where climatic changes lead to the slow extinction of its primary host. The species would then be left to specialize on the secondary host, and, in time, would diverge sufficiently so that it would be unable to utilize the original host, or would be competitively excluded from it by the presence of the parent species when contact is re-established. Such a pattern could have been followed in several groups of *Rhagoletis* which now have allopatric sibling species associated with different hosts in the eastern and western parts of North America (i.e., *pomonella* and *zephyria*, *cingulata* and *indifferens*, and possibly *tabellaria* on *Vaccinium* and *tabellaria* on *Cornus*).

A second possibility, suggested by Mayr (1963, p. 462), involves a shift from a primary to a secondary host in temporarily isolated peripheral populations before the original host is entirely extinct. Adaptation to the new host under these conditions could be rapid. It could also account for sympatric sibling species encountered in certain species groups of *Rhagoletis* (i.e., *pomonella*, *mendax*, and *cornivora* in the *pomonella* group; *cingulata*, *osmanthi*, and *chionanthi* in the *cingulata* group).

Although allopatric speciation can satisfactorily account for the origin of all sympatric sibling species in this genus, a second pattern of evolution involving allochronic speciation is also open to certain univoltine phytophagous species with rather narrow host requirements (Smith, 1941). Special-

ization on a few host plants has the advantage of reducing interspecific competition, but also means that the species must be more closely attuned to the seasonal cycle of the host than would an insect infesting a wide range of plants.

In a cold temperate region, plants have definite flowering and fruiting times. Most *Rhagoletis* species must emerge at a certain time each year to insure the presence of the greatest number of suitable oviposition sites. It is not surprising, therefore, that many univoltine phytophagous insects in a temperate climate have relatively sharp peaks of abundance during the summer months. A few flies, however, emerge as much as a month early or late during periods when the host is not generally available for oviposition. This habit of early and late emergence, coupled with the fact that many *Rhagoletis* species oviposit freely in non-host plants, could greatly facilitate allochronic speciation which might occur in the following way.

If eggs are deposited and larvae are able to develop in a non-host native plant, or one that has been recently introduced, a population may become established on the new host. At least three alternatives are open to this population. (1) If the optimum stage for oviposition and larval development of the new host coincides with that of the old host, the species may simply expand its ecological amplitude to include the new host, or (2) it may become an ecologically polymorphic species with distinct host races (Ludwig's theorem, see Mayr, 1963). (3) If the stages of development of the new host and old host do not coincide, the resulting population on the new host may build up to such large numbers in relative isolation that gene flow between the two populations, if it does occur, is greatly reduced or negligible. This would permit the new population to adapt itself rapidly to the new host. The degree of allochronic isolation would naturally regulate the amount of gene flow,

which is the critical factor in determining the rate and degree of divergence.

It should be pointed out that for two allochronic populations to become established it would not be necessary for the initial infestation on the new host to be temporally isolated from the parent population. A small population could first become established on a few late maturing varieties of the new host. Selection would then favor flies with genotypes associated with early emergence, as early emerging flies would find a more abundant host supply available for oviposition. This shift would probably occur rapidly and end when peak emergence coincided with the peak maturation period of the new host. The net result would be exactly the same as in the case where the original population became established from early emerging flies.

There is now some evidence that, under certain conditions, host races and even species of phytophagous insects may be formed in a relatively short period of time (Smith, 1941; Andrewartha and Birch, 1954; Zimmerman, 1960; Mayr, 1963). Rapid host race formation has occurred in several *Rhagoletis* species within the last hundred years, probably through allochronic isolation.

There is fairly good evidence that the apple race of *R. pomonella* originated about 1860 in the Hudson River Valley from a *Crataegus*-infesting population (see *Hosts* of *R. pomonella*), and within 40–50 years spread west to Minnesota, south to North Carolina, and northeast to Nova Scotia (Illingworth, 1912; O'Kane, 1914; Porter, 1928). The apple race now shows a decided preference for fragrant summer and fall varieties of apples, and, although early reports record infestations in late maturing varieties, it is now rarely recovered from such fruits (Illingworth, 1912; O'Kane, 1914; Dirks, 1935). Today, the varieties preferred by the apple race mature considerably earlier than do the fruits of *Crataegus* infested by the haw form, but

the amount of overlap between the times of emergence of the two has never been accurately established.

The first population on apples may have originated from only a single pair of early emerging flies from a local haw population, or could also have occurred via one or more females from the haw population ovipositing in late apples followed by a shift in emergence to coincide with the time of greatest fruit abundance.

A similar shift to a new host is presently occurring in the California population of *indifferens* whose normal host is *Prunus emarginata*, or pin cherry. This plant grows in great abundance in northern California and is heavily infested with the western cherry fruit fly. The cultivated cherry, which matures much earlier than the pin cherry, is normally not infested. A cherry orchard may be completely surrounded by pin cherry but remain entirely free from attack by this fly. Occasionally, however, late maturing cultivated cherries may be infested by early emerging pin-cherry flies. The California State Department of Agriculture's effective eradication program has never permitted these newly established populations to build up. Without continued surveillance, it is very likely that a permanent population of *indifferens* associated with cultivated cherries would rapidly become established as it has in Oregon and Washington.

The possibility of two species arising sympatrically from a single population of flies, therefore, is a definite possibility and needs further investigation. The importance of reducing gene flow between the two host races cannot be overstressed. Without a drastic reduction of gene flow, it seems unlikely that isolating mechanisms could be established readily. Just how drastic the reduction of gene flow must be naturally depends on the intensity of selection.

It should be noted that allochronic speciation and race formation probably would not be open to many tropical or subtropical phytophagous insects since annual periodic-

ity, at least in the Tropical Belt, is often extended over longer periods of time (Richards, 1952), and insects are usually multivoltine. Secondary hosts are almost an absolute necessity for these tropical species. This may explain why tephritids capable of infesting a multitude of host plants are restricted to tropical and subtropical regions. Apparently it is most advantageous for the univoltine, temperate climate species to become specialists. Host diversity in tropical representatives of Tephritidae is probably more greatly influenced by interspecific competition than by the ability to survive in other hosts.

Genus *RHAGOLETIS* Loew

- Rhagoletis* Loew, 1862, Europ. Bohrf., p. 44. [Monotypic; type (not examined, location unknown): *Musca cerasi* Linnaeus.] —Coquillett, 1910, Proc. U.S. Nat. Mus., 37: 599 (type, *Musca cerasi* Linnaeus). —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 14–15 (key to species, bibliography). —Hendel, 1927, In Lindner, Flieg. Pal. Reg., 5: 20, 74 (key to Palearctic species, description). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 401–404 (key to North American species, description). —Curran, 1932, Amer. Mus. Nov., 526: 3–4 (key to North American species, description). —Aczél, 1954, Dusenja, 5: 75–78 (description, key to Neotropical species). —Rohdendorf, 1961, Ent. Obozr., 40: 176–201 (key to Palearctic species).
- Zonosema* Loew, 1862, Europ. Bohrf., p. 43. Two species included; type species (not examined) = *Trypeta meigenii* Loew, designated by Coquillett, 1910, Proc. U.S. Nat. Mus., 37: 622. —Rohdendorf, 1961, Ent. Obozr., 40: 189 (key, description).
- Spilographa* Schiner, 1868 (in part), Reise der Novara, 2: 264–265 (*Spilographa* = *Zonosema* group).
- Carpomyia*, —Rondani, 1870, Boll. Soc. Ent. It., 99: 6.
- Microrrhagoletis* Rohdendorf, 1961, Ent. Obozr., 40: 187. [Monotypic; type (not examined): *Microrrhagoletis samojlovitshae* Rohdendorf, Bostandik District, southern Kazakhstan, USSR (LZI). NEW SYNONYMY.]
- Megarrhagoletis* Rohdendorf, 1961, Ent. Obozr., 40: 197. [Monotypic; paratype examined: *Megarrhagoletis magniterebra* Rohdendorf, southern Kazakhstan, USSR (LZI). NEW SYNONYMY].

Species not referable to Rhagoletis. Several species have been placed erroneously in *Rhagoletis* and the following list includes all the trivial names of these species as well as their accepted generic status at present.

caurina Doane = *Urophora formosa* (Coquillett)⁶

formosa Coquillett = *Urophora formosa* (Coquillett)

grindeliae Coquillett = *Urophora grindeliae* (Coquillett)

minuta Snow = *Procecidochares minuta* (Snow)

sapporensis Matsumura = *Matsumurania sapporensis* (Matsumura)

Generic diagnosis. Members of the genus *Rhagoletis* may be distinguished from other Trypetini by the presence of the following combination of characters: (1) ivory to yellowish white notopleural stripe reaching from humeral callus to the wing base; (2) wing pattern consisting of transverse yellow to brownish black bands; (3) r-m at center of 1st M₂; (4) frons slightly wider at vertex than at antenna but narrower than maximum width of eye; (5) gena about 0.12 to 0.23 height of head; (6) ocellar bristles approximately same length as upper fronto-orbitals; (7) three pairs of convergent lower fronto-orbitals, two pairs of reclinate divergent upper fronto-orbitals; (8) dorsocentrals located slightly before, on, or slightly behind line drawn between anterior supraalars, but always closer to anterior supraalars than to either transverse sulcus or acrostichals; (9) femora II and III without well developed spines along ventral margin; (10) male surstyli long and forcep-like, the prenisetae never apical or subapical.

Remarks. *Zonosema*, *Microrrhagoletis*, and *Megarhagoletis* synonyms of *Rhagoletis*. This revision follows Hendel's 1927 treatment of the genus *Rhagoletis* in which

he regarded the predominantly Palearctic *Zonosema* Loew to be a synonym of *Rhagoletis* Loew. Collin (1947) considered these as distinct genera on the basis of wing coloration and habitus. However, when the wing patterns of *R. meigenii* (Loew), the type species of *Zonosema*, and the closely related *R. basiola* (Osten Sacken) and *R. alternata* (Fallen) are compared with *R. cerasi* (Linnaeus), the type species of *Rhagoletis*, it is obvious that the difference is only one of degree in infuscation (Stone, 1951). In considering *Rhagoletis* from North and South America, it also becomes apparent that habitus is no criterion for generic separation. *Zonosema* species resemble some of the Neotropical *Rhagoletis* more closely than they do their Eurasian congeners. Therefore, based on the characters proposed by Collin, there is no reason to consider *Zonosema* distinct from *Rhagoletis*.

Benjamin (1934) and Rohdendorf (1961) also have recognized *Zonosema*, but their arguments for generic recognition based on body coloration, head shape, female genitalia, and spination on R₄₊₅ are unwarranted. Complete intergradation of these characters between the two genera may be found in the New World *Rhagoletis*.

The light yellow body color regarded as typical of *Zonosema* occurs in both Nearctic and Neotropical *Rhagoletis* species which are closely related to entirely black forms (i.e., *R. juglandis*-*R. boycei* and *R. ferruginea*-*R. striatella*). In the case of setae on wing vein R₄₊₅, *Rhagoletis* from the Western Hemisphere may entirely lack setae on this vein (*pomonella* group) or may have only one or two at the junction of R₂₊₃ and R₄₊₅ (*cingulata* group, some members of the *suavis* group). In others, this vein is heavily setulose (some *suavis* group species, *R. striatella*, and most Neotropical species). Complete intergradation also occurs in the ratio of the length of the ovipositor and tergite VI, and no outstanding differences have been noted in the male genitalia.

⁶ See Foote, R. H., 1965, Family Tephritidae, p. 659, in Stone, A., et al. (eds.), A catalog of the Diptera of America north of Mexico. U.S. Dept. Agr. Handbook no. 276.

On biological grounds it would also seem unsound to recognize *Zonosema* as a distinct genus. Several species infest the same or closely related host fruits as certain members of the genus *Rhagoletis*.

The characters proposed by Rohdendorf to distinguish his monotypic genera *Microrrhagoletis* and *Megarrhagoletis* from *Rhagoletis* also do not appear sufficient for recognition at the generic level. He states that in body coloration both genera closely resemble *Rhagoletis* and that they are very much like *Zonosema* in head shape. Since *Zonosema* is a synonym of *Rhagoletis*, I can see no reason for retaining the two genera on the basis of these characters. Even the wing patterns of both genera are very similar to that of *R. cerasi* (Linnaeus). Furthermore, a host race (which may eventually prove to be a distinct species) of *R. cerasi* and the two new genera proposed by Rohdendorf infest the same host, *Berberis heteropoda* Schrenk.

Although Rohdendorf could find no differences between the male or female genitalia of *Microrrhagoletis* and *Rhagoletis*, he did consider the long ovipositor sheath of the female and long surstyli of the male in *Megarrhagoletis* of considerable taxonomic importance. The close similarity in all other characters, including host requirements, however, would indicate a rather close relationship. If generic status is to be based on characters such as the length of the ovipositor or ovipositor sheath without taking into consideration equally important characters, then a new genus should be created for *R. striatella* which has a short ovipositor sheath but an extremely long ovipositor. *R. striatella*, however, is closely related to species in South America which have much shorter ovipositors. For this reason, it is felt that the importance of this character has been given too much emphasis by Rohdendorf. Both genera should, therefore, be considered synonyms of *Rhagoletis*.

Status of Zonosemata, Carpomyia, and Rhagoletoides. The two genera most closely

related to *Rhagoletis* are *Carpomyia* A. Costa and *Zonosemata* Benjamin. In the present revision these genera are recognized as distinct from *Rhagoletis*, but as more becomes known of the Neotropical and northeastern Asiatic species of all three genera it may be necessary to synonymize both *Rhagoletis* and *Zonosemata* with *Carpomyia*.

The minute size of the ocellar bristles in *Carpomyia* is the only character that effectively separates it from *Rhagoletis* whose ocellar bristles are of normal size. One Asiatic species of *Carpomyia*, *C. schineri* Loew, has the ocellars of normal length, and should therefore be placed in the genus *Rhagoletis*. Male and female genitalia as well as the host relationships of *Carpomyia* are very similar to *Rhagoletis* and offer no suitable characters for generic recognition.

The light yellow color of *Carpomyia* and the black pattern on the dorsum of the thorax have been used by some authors to separate *Carpomyia* and *Rhagoletis*. Color, as already pointed out in the case of *Zonosema*, is of questionable value as a criterion of generic distinction. The status of these two genera is therefore debatable and in need of careful consideration. A study of the chromosomes of *Carpomyia* may help to clarify the relationship somewhat as it has between *Zonosemata* and *Rhagoletis*.

The major differences between *Rhagoletis* and *Zonosemata* are in the position of the dorsocentral bristles, the number of lower fronto-orbital bristles, and their chromosome morphology. The surstyli of the male genitalia of *Zonosemata* are also considerably shortened beyond the prensisetæ but in some ways resemble those of *R. striatella*.

In *Zonosemata* the dorsocentrals are located in line with the acrostichals, while in some *Rhagoletis*, such as *basiola* and *feruginea*, the dorsocentrals may be inserted well behind the anterior supraalars but are always nearer to the anterior supraalars than to the acrostichals.

The number of lower fronto-orbital bristles is not always a reliable character

for separating *Zonosemata* and *Rhagoletis* because these bristles vary in number among species in both genera. *R. striatella* infesting the solanaceous genus *Physalis*, for instance, frequently has four pairs of lower fronto-orbital bristles, the number usually found in *Zonosemata*, while both *Z. electa* and *Z. vittigera* occasionally have only three pairs of lower fronto-orbitals.

In addition to the position of the dorso-centrals, the karyotypes also provide a means of distinguishing between the two genera. The chromosomes of *Rhagoletis* are of two basic types. Most of the species have five pairs of metakinetically chromosomes and a single pair of acrokinetic dots. Members of the *pomonella* group have three pairs of metakinetically, two pairs of acrokinetics, and a pair of dot chromosomes. With the exception of the dots, the chromosomes are long and distinct and their kinetochores are well defined. The sex chromosomes, when visible, are not heteropycnotic. Two species of *Zonosemata* studied cytologically, *Z. electa* (Say) and *Z. vittigera* (Coquillett) (Bush, 1965), have 12 chromosomes with extremely long heteromorphic and heteropycnotic sex chromosomes. The autosomes are metakinetically, minute, and have a fuzzy appearance. The sex chromosomes do not completely disappear during interphase, but remain as a diffuse heterochromatic mass in the nucleus. These differences probably represent a considerable degree of divergence and offer supporting evidence for maintaining *Zonosemata* as a distinct genus.

It should be noted, however, that the karyotype of *R. striatella*, with its long acrokinetic sex chromosomes and small metakinetically autosomes, is somewhat reminiscent of the *Zonosemata* karyotype. This observation, coupled with the facts that both described species of *Zonosemata* and *R. striatella* infest related plant genera and also show similarities in the number of lower fronto-orbital bristles, head shape, and certain characteristics of the male genitalia, indicates a possible distant relationship.

The distribution of three recently described species of *Zonosemata*, two from Mexico and one from Jamaica (Bush, 1965), suggests that this genus has its home base in either Central or South America. *Zonosemata* is, therefore, probably of Neotropical origin, and its true relationships with *Rhagoletis* may be more firmly established as more solanaceous infesting species are uncovered in Central and South America.

Recently (1960), a third monotypic genus, *Rhagoletoides* Foote, was described and is regarded as a close relative of *Rhagoletis*. The host of *Rhagoletoides latifrons* (van der Wulp) is unknown, but I have frequently encountered this species in Mexico on buffalo burr, *Solanum rostratum* Dunal, a solanaceous plant with a wide distribution in western North America and the central highlands of Mexico. In all probability, *R. latifrons* represents another relative of *Rhagoletis* and *Zonosemata* associated with the Solanaceae. *Rhagoletoides*, however, can easily be distinguished from *Rhagoletis* by the distinctive surstyli shape of the male genitalia and by the well developed apodeme on the genital ring. Both sexes of this genus also have well developed anterior and posterior ventral rows of spines on the mid and hind femora. These characters are lacking in *Rhagoletis*, *Carpomyia*, and *Zonosemata*.

Description. A detailed description of the generic characters is offered here and will not be repeated in the specific descriptions. *Head* (Figs. 1-3): 1.1-1.2 times wider than high; subquadrate in profile; light yellow to yellowish orange with postcranial region and mentum yellow or marked with light brown to black; ocellar triangle light brown to black; vertex narrower than maximum width of eye; eye about 1.25-1.55 times higher than wide; frons convex in profile, prominent at antennae, slightly wider at vertex than at antennae; antennae 0.61-0.73 length of face; third segment more than twice length of second; genae moderately narrow, from 0.12-0.24 height of head. Postcranial re-

gion slightly concave; face only slightly concave in profile; foveae deep, carina well developed; third antennal segment usually with a sharp awl-shaped tip, rounded in some Palearctic and Neotropical species; epistome slightly upturned; postgenae moderately bulging. Three pairs of convergent and slightly proclinate black fronto-orbitals, their bases in line with base of long black innerventral; two pairs black reclinate, divergent upper fronto-orbitals their bases in line with base of antennae; upper pair two-thirds length of lower; ocellars strongly proclinate, divergent, approximately same length as upper pair of upper fronto-orbitals; outerventrals black, about two-thirds innerventrals; postorbitals yellow to black, short, one-third to one-fourth length outerventral; zero to five intraventrals; postocellars yellow or black, about same length as upper pair of upper fronto-orbitals; zero to three yellow to black postventrals; yellow to black genal bristle always present, rarely weak; yellow gular present or weakly developed, sometimes undifferentiated from scattered yellow and black setae on postgenae and gulamentum; scattered setae also on lower two-thirds of frons and along lower half of ptinial sulcus; minute setae scattered over surface of eye; usually two to five black setae along dorsal margin of first antennal segment; second segment with well developed black pedicular setae, medial surface covered with short black decumbent setae, outer surface bare except for short setae along apical margin; arista black grading to yellow at base, normally pubescent. Face usually minutely pubescent, lighter in color than rest of head. *Thorax* (Figs. 5-6): base color highly variable, ranging from light yellow to black; notopleural stripe ivory to light yellow reaching from humeral callus along metapleuron to wing base; scutellum flat, trapezoidal. Dorsum covered with short decumbent thin setae and usually white to yellow pollinose microtrichia, the latter sometimes forming a distinct pattern of stripes. Normally two pairs scapulars with

supernumeraries occasionally present, arranged in tandem behind normal pair; position of dorso-centrals variable, ranging from slightly in front of line between anterior supraalars to almost midway between anterior supraalars and acrostichals; one to two, rarely three, mesopleurals; pteropleural sometimes minute. *Legs* (Figs. 7-9): coxa I with scattered microtrichia on anterior surface, and one to two black bristles on ventro-anterior margin; coxa II with five to seven black bristles and several short light brown setae on ventro-anterior margin; coxa III with black bristle and short light setae. Trochanter I bare; trochanter II with two short distinct black setae on dorso-apical margin; trochanter III with several short setae. Femur I with two to three ill-defined rows of bristles on dorsal surface, one to two rows of bristles on ventro-posterior surface; femur II with or without three to five somewhat poorly differentiated semierect setae on mid-anterior surface; femur III with three to eight bristle-like setae on apical end. Tibia II with long apical spur; tibia III with single row of short stout bristle-like setae on outer surface. *Wing* (Fig. 4): pattern consisting of yellow to black crossbands. R_1 setulose over entire length, node bare; R_{4+5} bare or with setae on dorsal surface; zero to four setae dorsally at junction of R_{4+5} and R_{2+3} , rarely setulose ventrally; two stout bristles at subcostal break. Anal cell variable, usually drawn out to point along $Cu_2 + 2nd\ A$, occasionally blunt (Figs. 176-180); posterior crossvein at about mid-point of 1st M_2 . First vein ends before mid-point of wing; fourth vein ends before apex of wing. *Abdomen* (Figs. 10-13): tergites II-IV in male, II-V or VI in female usually with white pollinose band along posterior margin, entirely absent or greatly reduced in some species. Tergites covered with fine setae approximately color of areas from which they arise; long black bristles along posterior and lateral margins of tergites III-V in male and III-VI in female. Sternites II-IV with well developed internal

apodemes. *Genitalia: male* (Fig. 14)—epandrium globose, covered with long bristles; surstyli usually long and forcep-like, short and broad in some species but prenisetae never terminal or subterminal. Ejaculatory apodeme variable, usually fan-shaped at apex; apical margin of fan occasionally thickened. Genital ring circular, without apodeme. *Female* (Figs. 15–16)—length of ovipositor sheath and ovipositor highly variable. Ovipositor with two or three minute preapical setae (Fig. 15). Two to three globular or cylindrical spermathecae always covered with scale-like papillae. Two accessory glands. Ventral receptacle resembling a cluster of grapes partially surrounding a central, more heavily sclerotized stem (Fig. 181).

Key to North American Species of RHAGOLETIS

The following key may be used to distinguish most of the North American species of *Rhagoletis*. In groups which have sibling species and present special problems in identification, reference must be made to the discussion of the species group concerned before a determination can be made.

1. Scutellum concolorous cream to yellowish white without distinct spot 2
Scutellum with distinct cream to yellow circular or V-shaped scutellar spot 8
2. Wing pattern with small, triangular shaped intercalary band crossing cells R_1 and R_3 between medial and subapical crossbands (Fig. 212); body entirely yellow. Host: rose hips (*Rosa* spp.) *basiola* (Osten Sacken)
Wing pattern without intercalary band; body yellow or black 3
3. Wing pattern without basal crossband (Fig. 195); body entirely yellow. Host: walnut (*Juglans* spp.) *juglandis* Cresson
Wing pattern with basal crossband (i.e., Fig. 196); body yellow to black 4
4. Medial band normally not joined to subapical band (Figs. 192, 194, 196); if joined (Fig. 193), then body yellow to yellowish tan and postscutellum entirely dark brown or with dark brown horizontal stripes 5
Medial band broadly joined to subapical band (Figs. 191, 210); postscutellum entirely black or yellow, never brown or with vertical stripes 7
5. Veins R_{2+3} and R_{4+5} with horizontal fuscous markings between apical and subapical crossbands (Figs. 194, 196) 6
Veins R_{2+3} and R_{4+5} without fuscous markings in this area; wing pattern as in Figure 192, rarely as in Figure 193. Host: walnut (*Juglans* spp.) *completa* Cresson
6. Thorax and abdomen black; wing pattern as in Figure 194. Host: walnut (*Juglans* spp.) *boycei* Cresson
Thorax and abdomen predominantly tan to yellow; black markings limited to pleural and sternopleural areas; wing pattern as in Figure 196. Host: walnut (*Juglans* spp.) *zoqui* n. sp.
7. Body black, abdomen without white bands; wing pattern as in Figure 210. Host: sour and pin cherry (*Prunus* spp.) *fausta* (Osten Sacken)
Body yellow to yellowish tan; wing pattern as in Figures 190–191. Host: walnut (*Juglans* spp.) *suavis* (Loew)
8. Scutellar spot V-shaped, wing pattern as in Figure 209. Host: husk tomato (*Physalis* spp.) *striatella* van der Wulp
Scutellar spot oval or trapezoidal shaped 9
9. Apical band of wing forming a fork (Fig. 204), or upper prong of fork separated from apical band by hyaline area (Fig. 203); surstyli with apical tuft of long setae (Figs. 79–82) *cingulata* group
Apical band of wing entire; surstyli without apical tuft of setae 10
10. Basal crossband joined to medial crossband (i.e., Figs. 185 or 197) 11
Basal crossband not joined to medial crossband 13
11. Medial band joined to apical and subapical bands to form an F-shaped pattern (Fig. 185) *pomonella* group
Medial band not joined to either apical or subapical band 12
12. Male genitalia and aedeagus as in Figures 85, 101, 123; apex of phallosome with tubular sac (Fig. 123S); female with two globular spermathecae (Fig. 162). Hosts: dogwood berries (*Cornus* spp.), blueberries (*Vaccinium* spp.) *tabellaria* (Fitch)
Male genitalia and aedeagus as in Figures 86, 102, 124; apex of phallosome bare; three cone-shaped spermathecae (Fig. 165). Host unknown *persimilis* n. sp.
13. Apical band contiguous with costa over entire length (Fig. 202). Host: Oregon grape (*Mahonia* spp.) *berberis* Curran
Apical band separated from costa by hyaline area (i.e., Fig. 201) 14
14. Medial band joined to subapical band by

- infuscated region in cell R_5 (Fig. 200).
 Host unknown *ebbettsi* n. sp.
 Medial band not joined to subapical
 band 15
15. Usually with single mesopleural bristle;
 anal cell not sharply pointed (Fig. 176);
 posterior surface of head with black
 horseshoe-shaped pattern; aedeagus with
 setulose apical appendage (Fig. 127);
 Two cylindrical spermathecae (Fig.
 167). Host: currants and gooseberries
 (*Ribes* spp.) *ribicola* Doane
- Usually two to three mesopleural bristles;
 anal cell sharply pointed (Fig. 178);
 black band only across upper third of
 head, lower two-thirds yellow; aedeagus
 without apical appendage (Fig. 125);
 two globular spermathecae (Fig. 163).
 Host: juniper berries (*Juniperus* spp.)
 *juniperina* Marcovitch

POMONELLA SPECIES GROUP

The outstanding feature of this group is the close morphological similarity between the various species in contrast to their distinct host requirements. *R. pomonella*, the apple maggot, is probably the best known member of the group and is also one of the most economically important species of *Rhagoletis* in North America. In 1867 Benjamin Walsh described *Trypeta pomonella* from specimens reared from haws in Illinois and apples in Long Island, New York. This description followed shortly after the realization that *pomonella* was becoming a serious pest of apples in north-eastern United States, particularly in the Hudson River Valley. It is from this region that the apple infesting population is thought to have spread over eastern United States and Canada (see Illingworth, 1912, and O'Kane, 1914, for summary). Since that time, *pomonella*-like *Rhagoletis* have been reared from blueberries, huckleberries, dogwood berries, snowberries, and several other fruits.

There has been controversy over the status of these forms with such authors as Brues (1924), Cresson (1929), Thorpe (1930), and Pickett (1937) considering them as simply host races or, at most, sympatric subspecies. Others such as Curran (1932), Benjamin (1934), Hall (1938), and

Christenson and Foote (1960) have regarded all or some of the forms as distinct species.

The results of the present investigation show that, in the broad sense, *R. pomonella* actually includes at least four species and possibly more. Morphological differences are slight, and for this reason I have relied heavily on biological criteria for clues to the status of these "cryptomorphic" species.

The decision to recognize the four species now included in the *pomonella* group is based on the following observations.

(1) Crosses and forced oviposition experiments attempted by independent workers (Lathrop and Nickels, 1932; McAlister and Anderson, 1935; Pickett, 1937; Hall, 1938, 1943; Pickett and Neary, 1940) indicate that reproductive isolation between the most closely related sympatric species, *R. pomonella*, *mendax*, and *cornivora*, is essentially complete. The results of these experiments are summarized in Table 2. In the case of crosses attempted between *pomonella* and *mendax*, viable F_1 progeny were produced only between *pomonella* females $\times$ *mendax* males, but not in the reciprocal cross.

(2) There are slight but consistent morphological differences between sympatric populations of the three eastern species which could not be maintained if gene flow existed between them. An example of these differences may be seen in the Dice-Leraas diagrams of Figure 21, illustrating the difference in ovipositor length. It should be noted that there is no overlap in ovipositor length between northeastern *pomonella* and the sympatric populations of *mendax* and *cornivora*. The difference in ovipositor length between *mendax* and *cornivora*, although not as dramatic, is also interesting, and considering the small variability in related species, the difference is probably significant. These differences will be discussed more fully in the taxonomic treatment of each species.

(3) Differences in behavior and ecology have been demonstrated in *pomonella* and

TABLE 2. RESULTS OF CROSSES BETWEEN "HOST RACES" OF *Rhagoletis* IN THE *pomonella* SPECIES GROUP. COMPILED FROM 1) PICKETT (1937), PICKETT AND NEARY (1940); 2) HALL (1938, 1943); 3) MCALISTER AND ANDERSON (1935); 4) LATHROP AND NICKELS (1932).

HOST OF ♂	HOST OF ♀	OVIPOSITED ON	PUPAE RECOVERED	AU- THOR(S)
apple	apple	apple or haw	+	1, 2
apple	apple	blueberry	+	1, 4
haw	haw	apple or haw	+	1, 2
haw	apple	apple or haw	+	1
apple	haw	apple or haw	+	1
blueberry	blueberry	blueberry	+	1, 3
blueberry	apple	apple or blueberry	+	1, 3
apple	blueberry	apple	—	1, 3
apple	blueberry	blueberry	—	1, 3
haw	blueberry	haw or blueberry	—	1
blueberry	haw	haw or blueberry	—	1
<i>Cornus</i>	<i>Cornus</i>	<i>Cornus</i>	+	2
<i>Cornus</i>	<i>Cornus</i>	apple or haw	—	2
<i>Cornus</i>	apple or haw	no mating	—	2
apple or haw	<i>Cornus</i>	no mating	—	2
apple or haw	apple or haw	<i>Cornus</i>	+	2

mendax, and are illustrated in the following examples.

Females of *mendax* are known to have great difficulty ovipositing in apples or haws (Lathrop and Nickels, 1932; Pickett, 1937). On the other hand, *pomonella* from apples will readily oviposit in blueberries in the laboratory, but a larva usually needs more than one blueberry to complete development (Lathrop and Nickels, 1932), a difficult hurdle to overcome in the field except perhaps under exceptional conditions (McAlister, 1932). Also, when second instar *mendax* larvae are transferred from blueberries to haws or apples (first instar larvae die), the resulting pupae and adults are of normal size for *mendax* (Lathrop and Nickels, 1932). This indicates that, in the case of *mendax*, size for the most part is probably determined by the genotype of the species and not by nutrition.

Another outstanding difference between these two species is the method of egg deposition. *R. mendax* places the egg directly beneath the skin of the berry, while *pomonella* inserts the egg well into the flesh of the fruit, usually to a depth equivalent to the full length of the ovipositor (Lathrop and Nickels, 1932).

The biology of *cornivora* has not been studied in any detail. However, *pomonella* has been induced to oviposit in dogwood berries under laboratory conditions and the resulting adults were smaller than normal. *R. cornivora*, which normally oviposits in dogwood berries, refused to oviposit in apples. This indicates that these two species have quite different host preferences.

Diagnosis. Members of the *pomonella* group form a well delineated complex of species distinguished from all other species groups in the genus by their distinctive karyotype, wing pattern, and bicolored halteres. Unlike the five pairs of metakinetic and a single pair of acrokinetic dot chromosomes found in most other groups, all species in the *pomonella* group have only three metakinetic chromosomes plus two rod-shaped acrokinetic chromosomes and a pair of acrokinetic dot chromosomes. In the wing pattern, both the apical and subapical wing bands are joined to the medial band along the anterior margin of the wing; the medial band is broadly joined to the basal band along the posterior margin of the wing (Figs. 185–189). The halteres are bicolored with the upper half black and the lower half yellow. In all

other *Rhagoletis* these structures are concolorous yellow to tan.

Description. Because of the slight morphological differences between species of the *pomonella* group, a detailed description of the whole group is presented, followed by a discussion and diagnosis of each species. Body and wing measurements are presented in Tables 3A–3B. *Head* (Figs. 22–26): a black horizontal stripe across postcranium; upper third of occiput and upper half of frontalia yellowish brown; lower half of frons and genae usually lighter golden yellow; parafrontalia, anterior region of postgenae, postorbital regions, and face light creamish yellow; antennae yellowish orange; mentum black. Postocellar, genal, and poorly developed gular bristles yellow; all other major bristles black; setae on postgenal region and gulamentum mostly yellow, with setae on genae and along basal margin of ptinial sulcus black; usually only one postvertical with 7 to 15 postorbitals. *Thorax* (Fig. 45): black except for cream colored notopleural stripe and circular scutellar spot. Dorsum covered with black and white short decumbent setae and white pollinose microtrichia arranged in four rows; outer row reaching from scapulars posteriorly to a point in line with base of prescutellars; medial row reaching only to a point midway between dorsocentrals and prescutellars; medial rows separated by a wide black band; two pairs yellow scapulars; dorsocentrals in line with anterior supraalars; two mesopleurals, lower usually shorter than upper. Postscutellum shining black; halteres with upper half black, lower half yellow. *Legs*: coxa I yellow on anterior surface, black on posterior surface; coxae II and III black. Femur I variable in color with anterior surface always light yellow to yellowish orange, posterior surface yellow or heavily marked with black; femora II and III dark brown to black except for yellow to yellowish orange knees. All tibiae yellow to yellowish orange; tibia III sometimes with brown or black shading particularly near base. Tarsal segments

entirely yellow to yellowish orange. *Wing* (Figs. 185–189): in transmitted light basal band joined broadly to medial band along $Cu_2 + 2nd\ A$. Medial band joined to apical band in cell R_1 and R_3 , and to subapical band in cells R_5 and part of cell 1st M_2 ; hyaline area between apical band and costa narrow at junction of R_1 and costa, but broadening posteriorly. Anterior margin of apical band smooth (Fig. 188) or broken in step-like fashion (Fig. 186). Width of subapical band variable with species. R_{4+5} bare over entire length and at junction with R_{2+3} . Anal cell pointed. *Abdomen* (Figs. 47–48): all segments black; tergites II–IV in male (Fig. 47) and II–V in female (Fig. 48) with white pollinose band along posterior margin. Band on tergite V in female sometimes reduced or, rarely, entirely absent. *Genitalia*: male—epandrium black; surstyli golden yellow, variable in shape depending on species. Aedeagus (Figs. 113–116) with long recurved finger-like apical appendage covered with long setae; vesica usually bifurcate. Ejaculatory apodeme normal (Figs. 135–138). *Female*—variation in ovipositor length shown in Figure 21; two minute preapical setae on ovipositor; ovipositor sheath brown to shining black. Three cylindrical spermathecae covered with long scale-like papillae (Fig. 156), two (one usually shorter than the other) on right side of abdomen, a single spermatheca on left side; apical third of spermathecae usually bare.

Rhagoletis pomonella (Walsh)

- Trypeta pomonella* Walsh, 1867, Amer. J. Hort., 2: 338–343. [Syntypes examined: lectotype ♀, by present designation, Ill. (Loew Coll.) (MCZ, Syntype No. 25702); ♀, no locality (Osten Sacken Coll.) (MCZ, No. 25702).]
Trypeta (Rhagoletis) pomonella, —Loew, 1873, Smithson. Misc. Coll., 256: 265–268 (description).
Rhagoletis pomonella, —Snow, 1894, Kansas Univ. Quart., 2: 164, pl. 6, fig. 3 (description).
 —Doane, 1898, Ent. News, 9: 69 (syn. *R. zephyria* Snow). —Aldrich, 1909, Canad. Ent., 41: 72, pl. 4, fig. 4 (in key, discussion). —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 7, 15–16, 18–19. —Curran, 1924, Rept. Ent.

Soc. Ontario, 54: 56-57 (taxonomy of host races). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 409-410, pl. 16, fig. 7 (taxonomy). —Curran, 1932, Amer. Mus. Nov., 526: 6-8, fig. 2 (taxonomy). —Benjamin, 1934, U.S. Dept. Agr. Tech. Bull., 401: 9, 12, fig. 13 (taxonomy, in Florida). —Pickett, 1937, Canad. J. Res. (D), 15: 54-60 (crossbreeding host races, male genitalia). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 61, 64, 66, 67, 69-72, figs. 28, 73, 133, 134, 175 (larval morphology, in key).

R. pomonella usually infests only fruits of the subfamily Pomoideae (Rosaceae), which includes several closely related genera (see *Hosts*). The single exception to this essentially oligophagous habit is a "host race" associated with wild and cultivated plums (*Prunus* spp., subfamily Prunoideae). This population may already have reached the species level, but further study is necessary to establish its status with certainty.

Benjamin (1934) noted that Florida specimens reared from wild plums were much smaller than those reared from haws; but he found that adults which emerged from pupae sifted from soil beneath infested plum trees closely approximated the size of specimens reared from *Crataegus*. He attributed this size difference to a deterioration in the nutritive qualities of plums after they had been picked.

In examining the specimens used by Benjamin in his revision, I have also found a distinct difference in body size and ovipositor length between the plum and haw populations (Fig. 21; Tables 3A-3B). However, I was unable to locate enough specimens that had emerged from pupae collected under infested plum trees to confirm Benjamin's observation that the method of rearing may influence body size.

In the absence of sufficient biological and distributional information, it is impossible to satisfactorily evaluate these slight differences and resolve the status of the plum and haw forms. Therefore, the two populations will be considered conspecific in this revision.

It should also be noted that there is an indication that the apple and haw forms may be diverging rapidly. A significant difference in ovipositor length between the two populations collected within 15 miles of each other in Nova Scotia suggests that they are already fairly restricted to their respective hosts (Fig. 21). These flies were captured on the host plant to eliminate any effects of rearing technique. Furthermore, the similarity in ovipositor length between *pomonella* on apples in widely separated areas and a correspondingly large variation in this structure between allopatric haw populations supports the conclusion reached by past workers that the apple infesting form originated from a single population in eastern United States and spread to other localities. Again, the lack of information makes it necessary to consider these two populations conspecific.

It is uncertain whether the *pomonella*-like flies reared from other genera of Pomoideae are conspecific or represent distinct host races or species. Nicholson (1929-30) noted the small size of three specimens reared from *Aronia arbutifolia* (L.) L. f. in Florida. The *pomonella* specimens I have examined reared from *Cotoneaster* (*Pyracantha*) sp. from Beaumont, Texas, are also very small, averaging smaller than *mendax* and *zephyria*. *Cotoneaster*, like the apple, is an introduced plant and cannot be considered a native host. These host populations warrant careful investigation as they offer an opportunity to study the process of speciation of phytophagous insects under natural conditions.

Diagnosis. The northeastern and Mexican populations of *pomonella* infesting *Crataegus*, *Pyrus*, *Prunus* (plums), and possibly *Aronia* and *Amelanchier*⁷ can be distinguished from *cornicora*, *mendax*, and *zephyria* by ovipositor length (Fig. 21), shape and proportions of the surstyli (Table 4; Figs. 71, 90), large body size (Tables

⁷ Adults have not been reared from *Amelanchier*. For discussion of material reared from *Aronia* see *Hosts*.

	<u>R. pomonella</u> Nova Scotia	<u>R. pomonella</u> Fla.	<u>R. pomonella</u> Texas	<u>R. pomonella</u> Mexico	<u>R. mendax</u> NE	<u>R. mendax</u> Fla.	<u>R. zephyria</u>	<u>R. cornivora</u>
	10	5	4	10	10	10	10	7
HL	1.00 [±] .017 (.91-1.08)	.90 [±] .010 (.79-.97)	.92 [±] .012 (.81-.93)	.91 [±] .025 (.78-1.03)	.76 [±] .013 (.69-.82)	.79 [±] .012 (.72-.87)	.78 [±] .021 (.63-.85)	.81 [±] .011 (.73-.91)
HW	1.54 [±] .028 (1.30-1.63)	1.50 [±] .019 (1.37-1.59)	1.04 [±] .016 (.88-1.24)	1.53 [±] .030 (1.35-1.65)	1.24 [±] .027 (1.11-1.33)	1.27 [±] .020 (1.12-1.36)	1.23 [±] .037 (1.00-1.38)	1.38 [±] .015 (1.26-1.52)
HH	1.41 [±] .014 (1.22-1.32)	1.23 [±] .015 (1.12-1.30)	.96 [±] .011 (.88-1.05)	1.29 [±] .030 (1.13-1.40)	1.03 [±] .028 (.86-1.16)	1.09 [±] .013 (1.00-1.13)	1.07 [±] .035 (.83-1.17)	1.16 [±] .012 (1.08-1.24)
FL	1.75 [±] .011 (1.73-.85)	.75 [±] .010 (.68-.84)	.75 [±] .010 (.68-.84)	.91 [±] .010 (.68-.86)	.61 [±] .013 (.56-.67)	.61 [±] .013 (.56-.71)	.61 [±] .019 (.53-.67)	.63 [±] .011 (.62-.77)
FW	1.01 [±] .015 (.88-1.16)	.70 [±] .010 (.70-1.00)	.70 [±] .010 (.59-.80)	1.04 [±] .025 (.82-1.14)	.85 [±] .020 (.75-.83)	.89 [±] .014 (.79-.95)	.88 [±] .026 (.77-.97)	.94 [±] .011 (.88-1.06)
EW	1.57 [±] .004 (1.44-.57)	.40 [±] .010 (.47-.54)	.40 [±] .010 (.31-.49)	.46 [±] .012 (.39-.49)	.42 [±] .010 (.37-.49)	.41 [±] .008 (.35-.44)	.43 [±] .015 (.35-.51)	.51 [±] .011 (.47-.67)
EH	1.57 [±] .003 (1.33-.59)	.71 [±] .010 (.42-.54)	.71 [±] .010 (.42-.54)	.54 [±] .010 (.49-.57)	.44 [±] .012 (.37-.51)	.45 [±] .007 (.41-.49)	.45 [±] .014 (.37-.51)	.47 [±] .011 (.42-.53)
TL	1.77 [±] .013 (1.75-.83)	.77 [±] .010 (.68-.74)	.77 [±] .010 (.47-.77)	.75 [±] .021 (.62-.82)	.53 [±] .016 (.51-.67)	.61 [±] .013 (.53-.65)	.57 [±] .020 (.48-.67)	.60 [±] .011 (.62-.77)
GW	1.47 [±] .007 (1.33-.29)	.22 [±] .010 (.17-.24)	.15 [±] .010 (.17-.29)	.23 [±] .005 (.16-.24)	.13 [±] .004 (.10-.20)	.17 [±] .001 (.14-.20)	.20 [±] .003 (.15-.22)	.23 [±] .001 (.20-.27)
TL	2.03 [±] .020 (1.92-1.14)	1.77 [±] .010 (1.63-1.87)	1.77 [±] .010 (1.63-1.87)	1.93 [±] .046 (1.65-2.08)	1.53 [±] .033 (1.37-.75)	1.56 [±] .023 (1.42-1.71)	1.57 [±] .054 (1.24-1.73)	1.70 [±] .011 (1.50-1.91)
	24	10	5	21	24	10	10	6
WL	3.42 [±] .043 (2.55-3.90)	3.07 [±] .054 (2.38-3.22)	2.04 [±] .010 (1.46-2.50)	3.50 [±] .054 (3.09-3.90)	2.60 [±] .026 (2.26-2.82)	2.46 [±] .045 (2.26-2.71)	2.83 [±] .060 (2.81-3.15)	2.50 [±] .010 (2.50-3.60)
WW	1.87 [±] .022 (1.74-2.03)	1.72 [±] .026 (1.61-1.64)	1.29 [±] .010 (1.11-1.43)	1.92 [±] .011 (1.67-2.16)	1.47 [±] .043 (1.28-1.57)	1.39 [±] .025 (1.23-1.50)	1.64 [±] .013 (1.33-1.79)	1.84 [±] .011 (1.42-1.67)

Table 3A. Body and wing measurements of males of the pomonella species group. Figures represent mean, standard error, and range.

	<u>R. pomonella</u> Nova Scotia	<u>R. pomonella</u> Fla.	<u>R. pomonella</u> Texas	<u>R. pomonella</u> Mexico	<u>R. mendax</u> NE	<u>R. mendax</u> Fla.	<u>R. zephyria</u>	<u>R. cornivora</u>
n	10	10	6	10	10	10	10	6
HL	1.05 [±] .023 (.92-1.14)	.98 [±] .019 (.92-1.05)	.79 [±] .010 (.58-.77)	1.01 [±] .025 (.90-1.16)	.78 [±] .014 (.68-.84)	.78 [±] .018 (.68-.83)	.93 [±] .015 (.77-.90)	.87 [±] .011 (.70-1.03)
HW	1.66 [±] .027 (1.54-1.78)	1.64 [±] .023 (1.54-1.75)	1.24 [±] .010 (1.12-1.50)	1.67 [±] .036 (1.53-1.89)	1.26 [±] .026 (1.13-1.40)	1.28 [±] .035 (1.03-1.43)	1.30 [±] .026 (1.21-1.44)	1.35 [±] .011 (1.18-1.53)
HH	1.41 [±] .027 (1.30-1.52)	1.39 [±] .016 (1.27-1.43)	1.01 [±] .010 (.91-1.16)	1.34 [±] .013 (1.12-1.57)	1.06 [±] .028 (.90-1.20)	1.06 [±] .025 (.94-1.20)	1.12 [±] .020 (.97-1.26)	1.13 [±] .011 (1.02-1.26)
EW	.80 [±] .013 (.74-.86)	.80 [±] .007 (.74-.83)	.61 [±] .010 (.55-.71)	.82 [±] .013 (.74-.88)	.61 [±] .011 (.53-.65)	.66 [±] .016 (.55-.73)	.64 [±] .017 (.56-.70)	.65 [±] .011 (.56-.76)
EH	1.14 [±] .020 (1.05-1.22)	1.14 [±] .017 (1.05-1.19)	.83 [±] .010 (.75-.97)	1.11 [±] .026 (1.00-1.23)	.88 [±] .022 (.76-.98)	.91 [±] .026 (.75-1.03)	.90 [±] .021 (.82-1.02)	.95 [±] .011 (.81-1.07)
FW	.53 [±] .014 (.52-.65)	.55 [±] .008 (.52-.60)	.39 [±] .010 (.35-.47)	.53 [±] .023 (.44-.66)	.43 [±] .012 (.38-.49)	.43 [±] .011 (.35-.49)	.47 [±] .009 (.43-.52)	.48 [±] .011 (.41-.55)
AL	.57 [±] .013 (.52-.64)	.56 [±] .009 (.50-.60)	.43 [±] .010 (.41-.43)	.60 [±] .015 (.53-.63)	.46 [±] .011 (.41-.52)	.46 [±] .009 (.41-.50)	.46 [±] .010 (.40-.51)	.46 [±] .011 (.41-.50)
FL	.81 [±] .017 (.74-.89)	.81 [±] .013 (.75-.88)	.61 [±] .010 (.53-.73)	.64 [±] .020 (.74-.90)	.61 [±] .018 (.50-.68)	.62 [±] .017 (.52-.70)	.65 [±] .015 (.55-.72)	.69 [±] .011 (.53-.80)
GW	.27 [±] .011 (.23-.33)	.26 [±] .005 (.22-.28)	.17 [±] .010 (.14-.20)	.29 [±] .020 (.24-.36)	.18 [±] .006 (.16-.20)	.18 [±] .006 (.15-.21)	.21 [±] .005 (.17-.22)	.23 [±] .001 (.20-.26)
TL	2.30 [±] .047 (1.98-2.50)	2.13 [±] .034 (1.84-2.19)	1.62 [±] .010 (1.42-2.00)	2.24 [±] .061 (1.88-2.58)	1.68 [±] .035 (1.45-1.86)	1.64 [±] .033 (1.40-1.76)	1.65 [±] .053 (1.42-1.91)	1.81 [±] .011 (1.60-2.10)
n	24	10	7	19	24	10	10	6
WL	4.10 [±] .054 (3.34-4.43)	3.67 [±] .055 (4.03-3.41)	2.80 [±] .010 (2.59-3.18)	3.88 [±] .094 (3.21-4.75)	3.01 [±] .057 (2.36-3.44)	2.78 [±] .021 (2.35-3.02)	3.22 [±] .050 (2.76-3.58)	3.21 [±] .011 (3.01-3.56)
WW	2.25 [±] .027 (1.87-2.43)	2.07 [±] .036 (1.90-2.32)	1.52 [±] .010 (1.39-1.78)	2.17 [±] .051 (1.80-2.59)	1.72 [±] .033 (1.38-1.97)	1.59 [±] .030 (1.52-1.71)	1.88 [±] .032 (1.62-2.15)	1.85 [±] .011 (1.66-2.15)

Table 3B. Body and wing measurements of females of the pomonella species group. Figures represent mean, standard error, and range. *n = 4

TABLE 4. SURSTYLI RATIO AND ANGLE OF THE *pomonella* SPECIES GROUP. FOR METHOD USED IN MAKING MEASUREMENTS SEE FIGURE 239. FIGURES REPRESENT MEAN, STANDARD ERROR AND RANGE.

SPECIES	LOCALITY	n	RATIO	ANGLE A
<i>pomonella</i>	all pop.	21	.81 ± .014 (.68-.92)	143 ± 1.15 (134-153)
<i>mendax</i>	NE	10	.87 ± .019 (.75-.93)	139 ± 0.34 (135-146)
<i>mendax</i>	Fla.	6	.85 (.69-1.00)	146 (139-151)
<i>zephyria</i>	all pop.	16	.67 ± .020 (.50-.84)	160 ± 1.32 (153-169)
<i>cornivora</i>	NE	3	1.00 (.98-1.01)	139 (138-141)
<i>cornivora</i>	Fla.	3	.79 (.77-.82)	145 (142-157)

3A-3B), and ratio between the width of the medial and subapical crossbands (Table 5). Finally, the presence of heavy black shading on the posterior surface of femur I in *pomonella* offers a useful morphological character in differentiating between this species and the sympatric *mendax* and *cornivora*.

In Florida the females of *pomonella* cannot be distinguished readily from *cornivora* or *mendax* except on the basis of body size (Table 3B, i.e., thorax length). Ovipositor length and color pattern show considerable overlap in this region. Males may be distinguished on the basis of surstyli ratio (Table 4) and overall size (Table 3A). For biological reasons already outlined, the Florida representatives of these three species must be considered distinct even though preserved material cannot always be identified without suitable host data.

Geographical variation. Three trends in geographical variation are evident in *pomonella*. The most conspicuous is the pronounced reduction in size in the extreme southern limits of its range in eastern North America and Texas where xeromesophytic conditions prevail (for example, see Fig. 21; Tables 3A and 3B). *R. pomonella*

TABLE 5. MEDIAL AND SUBAPICAL CROSSBAND WIDTH RATIOS OF THE WING FOR THE *pomonella* SPECIES GROUP. FIGURES INCLUDE BOTH MALES AND FEMALES AS NO DIFFERENCE BETWEEN THE SEXES WAS NOTED. FOR METHOD OF MAKING MEASUREMENTS SEE FIGURE 238.

SPECIES	LOCALITY	n	RATIO
<i>pomonella</i>	NE	48	.43 ± .008 (.30-.56)
<i>pomonella</i>	Mex.	40	.39 ± .008 (.30-.48)
<i>pomonella</i>	Fla.	20	.43 ± .012 (.30-.53)
<i>mendax</i>	NE	40	.59 ± .008 (.51-.69)
<i>mendax</i>	Fla.	23	.47 ± .012 (.34-.60)
<i>cornivora</i>	NE	10	.53 ± .015 (.46-.60)
<i>cornivora</i>	Fla.	11	.48 ± .011 (.43-.55)
<i>zephyria</i>	NW	38	.54 ± .014 (.41-.72)

uella infesting haws and plums in Florida and *Cotoneaster* sp. in Texas may be no larger in certain body measurements than specimens of *mendax* or *cornivora* from Massachusetts. This trend is reversed in the Mexican population of *pomonella* which is only slightly smaller than the northeastern representative of this species.

The difference in size between the northeastern and southern populations of *pomonella* is sharp enough so that an ill-defined geographic division can be drawn between them, represented by a broad area in southern South Carolina and northern Georgia. This region is proposed only as a probable area of transition between the smaller sized Florida *pomonella* population and the larger sized northeastern populations. I have been able to examine only a few specimens of *pomonella* from these two states and they have not provided enough information to establish just where the shift may occur or if the two populations

are actually completely isolated from one another.

A second trend is toward a slight reduction in the intensity and distribution of black coloring in the most southern populations, although this is not as marked as a similar shift of color pattern noted in *R. cingulata*.

A third trend is apparent between Mexican and northeastern populations in the wing pattern. In specimens from Mexico there is usually a hyaline spot at the base of the apical band just apical of its junction with the medial band (Fig. 186). This spot was never found in the northeastern specimens examined, although this region may be somewhat lighter than the rest of the band in teneral individuals.

Chromosome number and morphology (Figs. 213–214). The diploid number is 12; the MCA number is 18 as there are three pairs of metakinetically chromosomes, two rod-shaped acrokinetic chromosomes, and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) were observed. A secondary constriction is usually present at metaphase in one arm of the shortest metakinetically chromosome.

Source of cytological material: *Crataegus* spp., Cambridge, Mass., Sept. 20, 1962; Mil Cumbres, Michoacan, Mexico, Sept. 9, 1961. *Pyrus Malus*, Kentville, Nova Scotia, Oct. 26, 1962; West Crampton, New Hampshire, Aug. 27, 1960; Zaqualtipan, Hidalgo, Mexico, Aug. 15, 1957.

Courtship behavior. I was unable to get this species or any other member of the *pomonella* group to perform normally in the laboratory, and I have not observed courtship in the field. Males may be seen patrolling apples and haws, and mated pairs are frequently seen on foliage near fruit.

Parasites. The following hymenopterous parasites have been recorded from *pomonella*: *Opius lectus* Gahan, *O. alloeus* Muesebeck (= *ferrugineus* of authors), *O. melleus* Gahan, *Aphaereta muscae* Ashmead (Bra-

conidae); *Galesus* sp. (Diapriidae); Eulophidae (specimen damaged, genus and species unknown); *Pattasson conotracheli* (Girault) (= *Anaphoidea* of authors). For further details, see Porter and Alden (1921), Middlekauff (1941), and Muesebeck (1956).

Hosts. The recorded hosts of *pomonella* are summarized in Table 6. Although *pomonella* has been found to infest several genera of the family Rosaceae, it may still be considered essentially oligophagous. With the exception of the population on plums, which may yet prove to be a distinct species (see introductory remarks), it is associated only with members of the subfamily Pomoideae. This group includes several closely related genera⁵ considered by some botanists to represent a single genus (Sax, 1931, 1933; Lawrence, 1951). Intergeneric graft hybrids and crosses have been made between many genera in this subfamily indicating a close relationship (see Weber, 1963, for summary).

The major hosts of *pomonella* in the Pomoideae are hawthorn (*Crataegus*) and apples (*Pyrus*), but not all varieties and species of these plants serve as hosts in the field or under laboratory conditions (Wellhouse, 1922; Porter, 1928; Pickett, 1937).

The association of *pomonella* with apples in both northeastern United States and Mexico is a recent one with the first recorded infestation published by Ward in 1866 (vide Illingworth, 1912), over 200 years after the introduction of the apple into New England from Europe. It is very likely that *pomonella* was infesting apples for several years before 1866 as Walsh (1867) reported infestations in this fruit from widely separated areas in the Hudson River Valley. It is not known when *pomonella* became established on apples in Mexico, but the first apple trees were planted in 1522 (Bustamente; vide Stand-

⁵ *Pyrus* (including *Malus*), *Crataegus*, *Sorbus*, *Aronia*, *Amelanchier*, *Cotoneaster*, and others

ley, 1922), about 100 years before their introduction into New England. The shift from a native host to apples probably occurred independently in these two areas as both populations on apples have maintained the distinct wing pattern of the parent *Crataegus* population.

The question of the original native host of the apple population has never been adequately answered. The most logical suspect in eastern United States would be the native wild crabapples. However, native crabs have never been found infested with *pomonella* (O'Kane, 1914; Porter, 1928), but introduced Siberian crabs such as *Pyrus baccata* L. and *baccata* $\times$ *Malus* hybrids are readily attacked (Ross, 1913; O'Kane, 1914). The reason for this preference has not been studied, but it has been suggested that the fruit of most North American species ripens too late for *pomonella* to complete its development before winter sets in (O'Kane, 1914). Apparently there is also a considerable difference between Siberian and North American crabs as attempts to hybridize the two have never been successful (Wood, personal communication). On the other hand, native crabs and apples do hybridize (McVaugh, 1943), but it is not known if these hybrids become infested with *pomonella*.

The absence of native crabs in Mexico and the presence of infested *Crataegus*, coupled with the observation that native crabs are not attacked in northeastern United States, indicate that the shift occurred from *Crataegus* to apples in both regions. *Crataegus*, therefore, is the most likely original native host of the apple population.

The single exception to the host specificity of *pomonella* for members of the Pomoideae is the "host race" on wild and cultivated plums (*Prunus*, subfam. Prunoideae). The distribution of *pomonella* in relation to this host is not well known. The reported infestations from Florida (Benjamin, 1934) and New York (Greene, 1927), as well as an examination of a series of

specimens reared from plums in New Brunswick, Canada, indicate that this race is distributed over most of the range of the native plum species.

The peach, *Prunus persica* (L.) Batsch, has also been recorded as an occasional host of *pomonella* (Porter, 1928), but apparently infestations are rare, have never reached economic proportions, and occur only when peaches are growing near infested apples. This introduced plant therefore cannot be regarded as a normal host for *pomonella*.

Distribution (Map 1). *R. pomonella* is limited to areas east of the 100th meridian along the transitional zone, except for an occasional introduction into apple growing regions of the West. It reaches north only to the most southern part of the eastern Canadian provinces and south to eastern Texas and northern Florida. This species is also found in the central highlands of Mexico but the exact limits of its distribution in this country are unknown.

Map 1 shows the distribution of the two major native host genera, *Crataegus* and *Prunus*. All the known species of both genera are lumped to show the known distribution of *pomonella* in relation to the potential host species.

It should be mentioned that *pomonella* may have a much wider distribution than present records indicate. In addition to the specimens I have reared from *Crataegus* and *Pyrus Malus* in Mexico, infested fruits of both genera have been intercepted from Mexico and Costa Rica (Benjamin, 1934; U. S. Dept. Agr. unpublished interception records). Apples are not grown commercially in Costa Rica, but *Crataegus*, although not native, grows as an escape at high elevations (Standley and Steyermark, 1946). *R. pomonella*-like larvae have also been found in apples growing in Colombia (Garcés and Gallego, 1947), but the extent of the infestation and accurate identification of the species involved have not been determined. *Crataegus* is not native to South America. It was introduced by In-



dians who used it as food (Standley and Steyermark, 1946); thus *pomonella* may have been introduced with the fruit.

Rhagoletis zephyria Snow

Rhagoletis zephyria Snow, 1894, Kansas Univ. Quart., 2: 164–165. [Described from 5 ♂♂, southern California (leg. Baron) (KU); lecto-type ♂ examined, designated by Foote, 1962; also examined: 3 ♂♂ (KU), 1 ♂ (MCZ, No. 7724).] —Doane, 1898, Ent. News, 9: 69 (in key, = *pomonella*). —Curran, 1924, Canad. Ent., 56: 62–63 (distinct from *symphoricarpi*). —Benjamin, 1934 (in part), U.S. Dept. Agr. Tech. Bull., 401: 9, 12 (syn. *symphoricarpi* with *zephyria*). —Pickett, 1937, Canad. J. Res. (D), 15: 56–57, figs. 4, 16, 17, 23, 25 (subspecies of *pomonella*). —Foote, 1962, J. Kansas Ent. Soc., 35: 178–179 (lecto-type designated).

Rhagoletis pomonella Aldrich, 1905 (in part), Smithson. Misc. Coll., 1444: 607 (in catalog, syn. of *pomonella*). —Aldrich, 1909 (in part), Canad. Ent., 41: 69 (syn. of *pomonella*). —Cresson, 1929 (in part), Trans. Amer. Ent. Soc., 55: 409–410 (syn. both *zephyria* and *symphoricarpi* with *pomonella*).

Rhagoletis symphoricarpi Curran, 1924, Canad. Ent., 56: 62–63. [Holotype ♂ not examined, Victoria, B.C., June 30, 1919, reared from *Symphoricarpos* (W. Downes) (CNC, No. 634); paratypes examined: 2 ♂♂ 1 ♀, Victoria, B.C., June 20; 2 ♂♂ 1 ♀, June 24; 1 ♂ 1 ♀, June 25, 1919, host *Symphoricarpos* (W. Downes) (CNC, No. 634); 1 ♂, Creston, B.C., no date or leg., host *Symphoricarpos* (CNC, No. 634); 1 ♀, Lytton, B.C., no date or leg., host *Symphoricarpos* (CNC, No. 634).] —Phillips, 1946, Mem. Ent. Soc. Amer., 12: 76–77, figs. 32, 77, 140, 179 (larval morphology, in key).

Diagnosis. *R. zephyria* is sympatric with *pomonella* only in the extreme eastern limits of its range. It can be distinguished from *pomonella* by surstyli shape (Figs. 69, 91; Table 4), ovipositor length (Fig. 21), wing band ratio (Table 5), and its exclusive association in the larval stage with snowberry (*Symphoricarpos*). Surstyli shape and host preference will also distinguish *zephyria* from all other described species in the *pomonella* complex. There is some similarity between *zephyria* and Florida *mendax* in the shape of the surstyli; however, those of *mendax* are more angled

in lateral view (Table 4) and not flared in posterior view (Figs. 91, 94).

Geographical variation. No geographical variation was noted in this species.

Chromosome number and morphology (Fig. 215). The diploid number is 12; the MCA number is 18 as there are three pairs of metakinetic chromosomes, two pairs of acrokinetic rod-shaped chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *Symphoricarpos* sp., Corvallis, Oregon, July 20, 1961; Forestville, California, Aug. 10, 1961.

Courtship behavior. The courtship behavior of this species was not studied.

Parasites. *Opius lectoides* (Gahan, 1930) is the only parasite recorded from *zephyria*. It has not been found associated with any other *Rhagoletis* species.

Hosts. *R. zephyria* has only been reared from *Symphoricarpos* (Caprifoliaceae) which is closely related to *Lonicera* (Jones, 1940), a genus infested by several European *Rhagoletis* species. Lathrop and Nickels (1931, 1932) state that *zephyria* has also been found in the fruits of blueberry and whortle berry in the western United States, but give no details regarding the source of their information. *R. tabellaria* is the only species known to infest *Vaccinium* in the West, and I have been unable to confirm the Lathrop and Nickels host record.

Symphoricarpos is almost entirely restricted to North America where 16 species are known. One species has been found in central China (Jones, 1940). There is a continuous distribution of various representatives of this genus over North America ranging from southeastern Alaska to central Guatemala.

R. zephyria has been reared from *S. rivularis* Suksdorf (*S. albus* and *S. racemosus* of authors; see Jones, 1940, for discussion of synonymy), whose distribution (Map 2) coincides fairly well with that of *zephyria*.



S. rivularis has been introduced and escaped from cultivation over a wide range in eastern North America, a fact which may account for the extension of the range of *zephyria* so far to the east.

Since this fly may infest other *Symphoricarpos* species, the approximate distribution of the genus in North America has also been shown.

Distribution (Map 2). This species ranges from southern British Columbia south to the central and possibly southern highlands of California, and east in southwestern Canada and northwestern United States to Minnesota.

Rhagoletis mendax Curran

Rhagoletis pomonella. —Britton, 1906, Conn. Agr. Expt. Sta. Ann. Rept. (1905), 29: 260 (infesting *Gaylussacia* in Conn.). —Phillips, 1923 (in part), J. New York Ent. Soc., 31: 136 (in cranberries). —Cresson, 1929 (in part), Trans. Amer. Ent. Soc., 55: 409–410 (taxonomic status). —Benjamin, 1934 (in part), U.S. Dept. Agr. Tech. Bull., 401: 9, 12 (taxonomy). —Pickett, 1937, Canad. J. Res. (D), 15: 53–75 (taxonomy, race of *pomonella*). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 70, figs. 27, 72, 131–132, 174 (larval morphology, in key).

Rhagoletis mendax Curran, 1932, Amer. Mus. Nov., 526: 6, 7. [Holotype ♂ examined (abdomen missing), Maine (A. D. Pickett) (AMNH); allotype ♀ and ♂ paratype examined, same data as holotype.]

Rhagoletis zephyria. —Benjamin, 1934 (in part), U.S. Dept. Agr. Tech. Bull., 401: 9, 12.

R. mendax was originally described by Curran (1932) from *pomonella*-like flies reared from blueberries in Maine. With the exception of Christenson and Foote (1960), current authors have not accepted Curran's recognition of *mendax* as a distinct species. Most entomologists continue to refer to this species only as a distinct race of *pomonella*, even though crossbreeding experiments have clearly shown that these two "races" are reproductively isolated (see Table 2). Moreover, the two species appear ecologically distinct with uninfested blueberries growing in the vicinity of heavily infested apples or hawthorns and

vice versa (Woods, 1915a; Lathrop and Nickels, 1932). *R. pomonella* also has a much more extensive westward range than *mendax*. Blueberries beyond Michigan are not known to be infested by this species. These facts, as well as others already pointed out in the discussion of the *pomonella* group, make it impossible to regard *mendax* as simply a race of *pomonella*.

Diagnosis. *R. mendax* north of Georgia may be distinguished from *pomonella* by the following combination of characters: (1) shorter ovipositor length (Fig. 21); (2) difference in wing band ratios (Table 5); (3) absence of black shading on the posterior surface of femur I; (4) larvae infest fruits of *Vaccinium*.

The problem of separating *mendax* from *cornivora* is more difficult. No crossbreeding experiments have been made between these two species. In Ontario, however, *Cornus amomum* is heavily infested with *cornivora*, but Hall (1943) was unable to find blueberries infested, indicating a definite host preference between the two species. There is probably a significant difference in ovipositor length but the number of *cornivora* specimens available for study was not sufficient to make a statistical comparison. The male genitalia may also furnish useful characters for separation as the surstyli ratio in *mendax* is much smaller than in *cornivora* (Table 4). Again, it should be stressed that the number of specimens examined was small. The allopatric species, *zephyria*, may be distinguished on the basis of surstyli shape (Figs. 67, 69, 91, 93) and host preference.

In Florida, *mendax* can be distinguished from *cornivora* and *pomonella* on the basis of host preference and by the shape (Fig. 70) and angle of the male surstyli (Table 4). Females, however, possess no morphological characters that can be used to separate them from females of the other two sympatric species.

Geographical variation. There is a distinct difference in the male genitalia between the Florida and northeastern popula-

TABLE 6. MEMBERS OF THE FAMILY ROSACEAE RECORDED AS HOSTS OF *R. pomonella*. L = LARVAE ONLY OBSERVED; A = IDENTIFICATION CONFIRMED BY REARING LARVAE TO ADULT STAGE.

SUBFAMILY	GENUS	SPECIES	LOCALITY	AUTHOR(S)	REMARKS
Pomoideae	<i>Crataegus</i>	<i>punctata</i> Jacq.	N.Y.	Wellhouse 1922	A
		<i>pedicellata</i> Sarg. (= <i>albicans</i>)	N.Y.	Wellhouse	A
		<i>Brainerdi</i> Sarg.	N.Y.	Wellhouse	A
		<i>pruinosa</i> (Wendl.) K. Koch	N.Y.	Wellhouse	A
		<i>macrosperma</i> Ashe	N.Y.	Wellhouse	A
		<i>melanocarpa</i> ?	N.Y.	Glasgow 1933	A
		<i>maloides</i> ?	Fla.	Nicholson 1929-30	A
		spp.	E U.S., SE Can.	O'Kane 1914	A
			Central Mex.	Bush (unpublished)	A
Pomoideae	<i>Pyrus</i>	<i>Malus</i> L.	E U.S., SE Can.	Authors 1868-1963	A
			Central Mex.	Bush (unpublished)	A
		<i>baccata</i> L.	Ont.	O'Kane 1914	A
		crabapple × <i>Malus</i> <i>communis</i> L.	N.H., Mich. Conn., Me.	O'Kane 1914 Porter 1928	A L
Pomoideae	<i>Aronia</i>	<i>arbutifolia</i> (L.) L.	Fla.	Benjamin 1934	A
		<i>melanocarpa</i> (Michx.) Me.	Me.	Lathrop and Nickels 1932	L
Pomoideae	<i>Amelanchier</i>	<i>Bartramiana</i> (Tausch) Roemer	Me.	Lathrop and Nickels 1932	L
Pomoideae	<i>Cotoneaster</i> (<i>Pyracantha</i>)	sp. ?	Tex.	USDA	A
Prunoideae	<i>Prunus</i>	<i>angustifolia</i> Marsh.	Fla.	Benjamin 1934	A
		<i>umbellata</i> Ell.	Fla.	Benjamin	A
		cultivated plum	N.Y., N.B.	Herrick 1920	A

tions of *mendax*. On this basis, Benjamin (1934) regarded the Florida *Vaccinium*-infesting population to be synonymous with *zephyria*, an allopatric species infesting an entirely different host. The male genitalia do bear some resemblance, but the distribution of the two species and difference in host requirements would rule out a close relationship. Divergence of the Florida *mendax* from the northeastern population probably occurred sometime during the Pleistocene when peninsular Florida was isolated from the mainland as a chain of islands. Since both populations of *mendax* utilize the same hosts, it seems inadvisable to consider the Florida form as a distinct species in the absence of crossing experiments and more detailed knowledge of the biology and distribution of both populations.

Two males from Bobcaygeon, Ontario (in the CNC), have been tentatively assigned to *mendax*. The genitalia of one specimen have been examined and the surstyli are very similar in shape to those found in Florida *mendax*. There are no records of *mendax* infesting blueberries in Ontario. In view of these facts, the identification of these specimens is in doubt.

Chromosome number and morphology (Fig. 216). The diploid number is 12; the MCA number is 18 as there are three pairs of metakinetin chromosomes, two pairs of rod-shaped acrokinetic chromosomes, and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *Vaccinium* spp., Northfield, New Hampshire, Aug.

TABLE 7. SPECIES OF ERICACEAE FOUND INFESTED BY *R. mendax*. REMARKS: L = LARVAE ONLY OBSERVED; A = IDENTIFICATION CONFIRMED BY REARING LARVAE TO ADULT STAGE. TAXONOMIC TREATMENT OF HOST PLANTS FOLLOWS CAMP (1941, 1945) AND WOOD (1961).

GENUS	SUBGENUS OR SECTION	SPECIES	LOCALITY	AUTHOR(S)	REMARKS
<i>Vaccinium</i>	<i>Cyanococcus</i>	<i>angustifolium</i> Ait. (= <i>pennsylvanicum</i> of authors)	Me., N.J.	Lathrop and Nickels 1932; Woods 1915a	A
		<i>canadense</i> Kalm	Me.	Woods 1915a	A
		<i>corymbosum</i> L.	Me., N.H., N.J.	Woods 1915a; O'Kane 1914	A
		<i>pallidum</i> Ait.	N.J.	teste Marucci	A
		spp.? (blueberries)	Mich.	Anonymous 1963	A
		<i>Formosum</i> Andr. (prob. <i>fasciatum</i> Ait.)	Fla.	Nicholson 1929-30	L
	<i>Batodendron</i>	<i>arborescens</i> Marsh.	Fla.	Benjamin 1934	A
	<i>Vitis-idaea</i>	<i>citis-idaea</i> L.	Me.	Lathrop and Nickels 1932	L
	<i>Oxycoccoides</i>	spp.? (cranberries)	N.S.	Phillips 1923	L(A?)
				Pickett and Neary 1940 Bush (unpublished)	L A
<i>Gaylussacia</i>	<i>Decamerium</i>	<i>baccata</i> (Wang.) K. Koch	Conn., Me., N.H.	Britton 1906; Woods 1915a; teste Marucci	A
		<i>frondosa</i> (L.) T.&G.	N.J.	teste Marucci	A
		<i>dumosa</i> (Andr.) T.&G.	N.J.	teste Marucci	A
<i>Gaultheria</i>	<i>Gaultheria</i>	<i>procumbens</i> L.	Me.	Lathrop and Nickels 1932	L

27, 1960; Yarmouth, Nova Scotia, Sept. 7, 1962; vicinity of Wilcox, Florida, June 29, 1962.

Courtship behavior. The courtship behavior of this species was not studied.

Parasites. The following parasites have been reared from *mendax* in Maine: *Opus melleus* Gahan (= *Biosteres rhagoletis* Richmond of Woods, 1915b) and *O. richmondi* Gahan (Lathrop and Nickels, 1932) (Braconidae). Apparently *O. melleus* is by far the more frequently encountered parasite. Parasitism averages about 10.7 per cent.

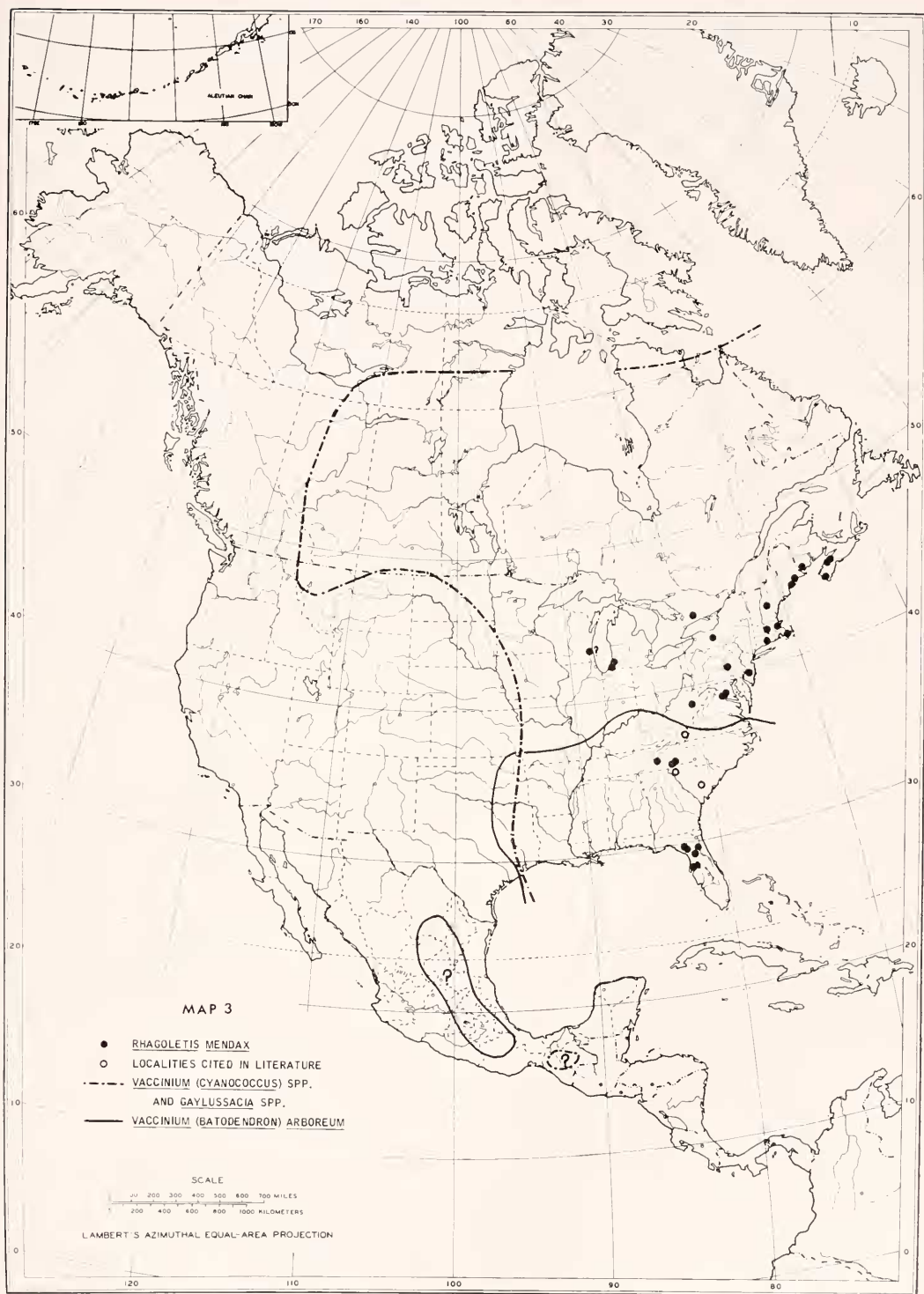
It has also been stated that adults of *O. melleus* parasitizing *mendax* are much smaller than *O. melleus* which parasitize *pomonella* (Lathrop and Newton, 1933). This suggests that two species of *Opus* may be associated with *mendax* and *pomonella*.

Hosts. Adults of *mendax* have been reared only from *Vaccinium* and *Gaylus-*

sacia (Ericaceae). Larvae identified as *mendax* have also been found in *Gaultheria procumbens* L. (wintergreen; Ericaceae), but adults have never been recovered. Table 7 outlines the species of plants with which *mendax* has been found associated. There is an apparent preference for *Vaccinium* and *Gaylussacia* whose fruits are similar in many respects. Wintergreen and cranberries do not appear to be suitable hosts for this species and I have examined only a few specimens reared from the latter host.

Host distribution is based on Camp (1941, 1945).

Distribution (Map 3). *R. mendax* is primarily restricted to northeastern United States and southeastern Canada. It has been reared from blueberries as far west as Michigan, and I have examined a single damaged specimen from Milwaukee, Wis-



consin, which I am tentatively regarding as conspecific. The second morphologically distinct population occurs in Florida and may be coextensive with the northern population, but insufficient collecting makes it impossible to establish its range with certainty.

Rhagoletis cornivora new species

Types. Holotype ♂, Lincoln, Mass., larva collected Sept. 10, 1962, ex *Cornus stolonifera* (G. L. Bush) (MCZ, No. 30828); paratypes: 3 ♂♂ 4 ♀♀, same data as holotype (MCZ, No. 30828).

Hall (1938, 1943) has shown through crossing experiments that *cornivora* is reproductively isolated from *pomonella* (Table 2). Apparently *cornivora* has difficulty ovipositing in apple and the larvae have not been reared from this fruit in forced oviposition experiments. Pickett (vide Hall, 1938) also noted consistent morphological differences between the surstyli of *cornivora* and other members of the *pomonella* group. He did not, however, regard them as important enough to consider the *Cornus*-infesting race a distinct species. Because the two sympatric "host races" are reproductively isolated and show morphological differences associated with host preference, it is necessary to consider the *Cornus* race a distinct species.

Two populations of *cornivora* showing slight but probably significant morphological differences in male and female genitalia have been found in Florida and the Northeast (see *Geographical variation*). These two populations are considered here to be conspecific. Eventually, when more biological data are available, they may prove to be different species.

Diagnosis. *R. cornivora* may be distinguished from the other sympatric members of the *pomonella* group (*mendax* and *pomonella*) north of Georgia by the surstyli shape and ratio (Table 4; Figs. 68, 92), ovipositor length (Fig. 21), and the host preference for *Cornus* spp. Also there is a slight difference in the morphology of

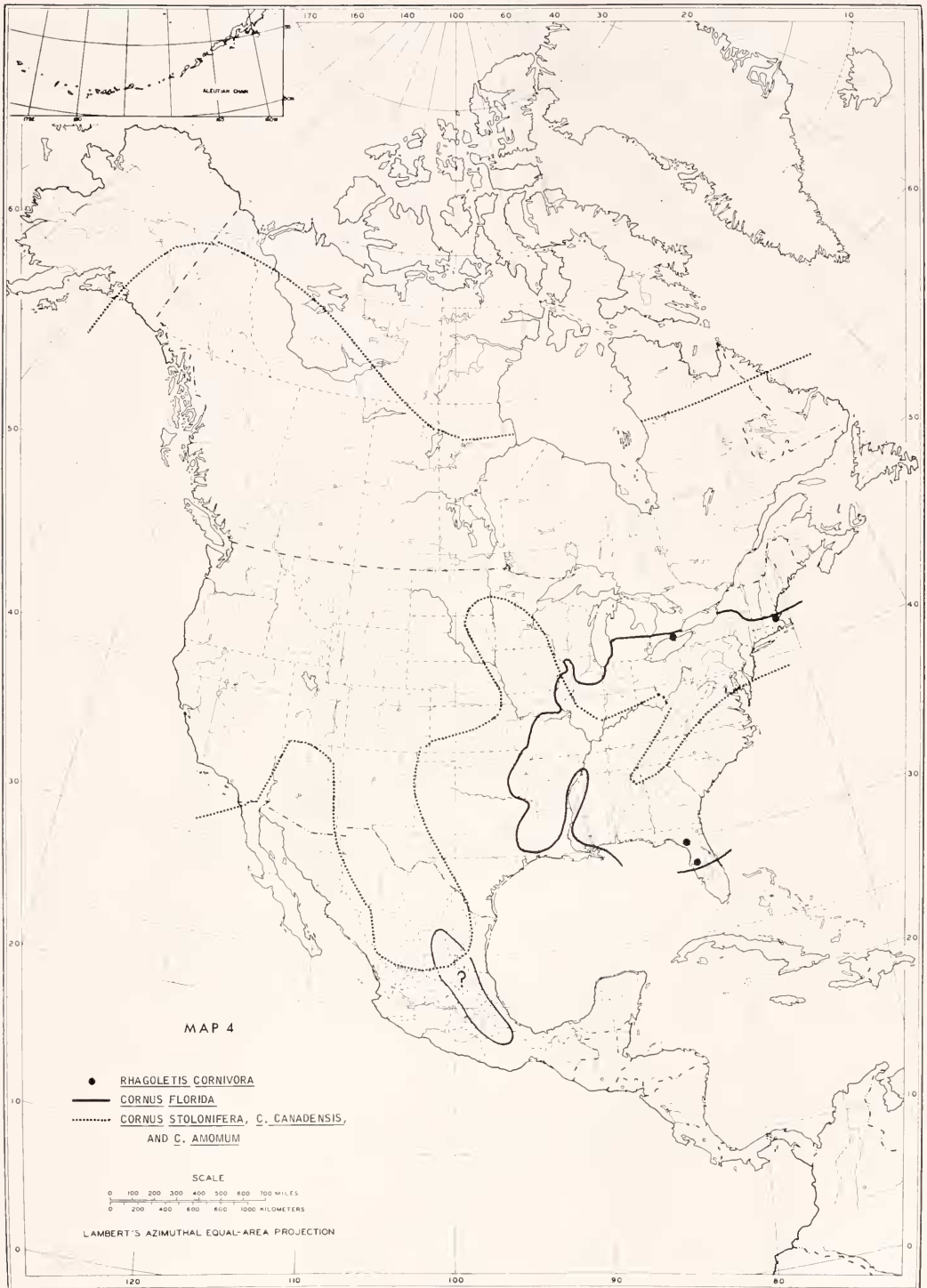
the meiotic chromosomes of *cornivora* and the other members of this group which may be used to identify the species if living material is available (see *Chromosome* section). Females of the Florida population of *cornivora* cannot be distinguished from *mendax* or *pomonella* without host data as there is considerable overlap in ovipositor length of all three species. There are no differences in the male genitalia of *cornivora* and *pomonella*.

Geographical variation. There is some variation between the Florida and northeastern populations of *cornivora* in ovipositor length and surstyli ratio. The northeastern populations have been reared from three species of *Cornus*, while Florida representatives have been reared only from *C. florida*. Also the trend toward reduction in size noted in *pomonella* is reversed in this species: adults of *cornivora* from Florida are considerably larger than those reared from *Cornus* in northeastern United States. This may be a true case of geographical variation, or perhaps two distinct species are involved. The answer will have to await further biological data.

Chromosome number and morphology (Fig. 217). The diploid number is 12; the MCA number is 18 in the female and 19 in the male. The male karyotype consists of a submetakinetik Y chromosome slightly longer than the acrokinetic X chromosome, a single pair of acrokinetic autosomes, three pairs of metakinetik autosomes, and a pair of dot acrokinetic autosomes. The female karyotype has a pair of acrokinetic X chromosomes, a single pair of acrokinetic autosomes, three pairs of metakinetik autosomes, and a pair of dot acrokinetic autosomes. No secondary constrictions were noted. The presence of the Y chromosome in the male was confirmed through a study of meiotic and spermatogonial figures in adult testes.

Source of cytological material: *Cornus stolonifera*, Lincoln, Mass., Sept. 13, 1960.

Courtship behavior. The courtship behavior of this species has not been studied.



Hosts. *R. cornivora* has been reared from the fruits of the following host plants: *Cornus canadensis* L. in Maine (Lathrop and McAlister, 1931), *C. anomum* Mill. in Ontario (Hall, 1938, 1943), *C. stolonifera* Michx. in Massachusetts, and *C. florida* L. in Florida (Benjamin, 1934). *R. cornivora*-like larvae have also been found in the fruits of *C. florida* on Plummer's Island, Maryland, indicating that this plant may serve as a host over most of its range. It is not known if *R. cornivora* occurs on the Mexican subspecies of *C. florida*.

Distribution. Map 4 shows the inclusive distribution of the three northeastern species of *Cornus* infested by *cornivora*. The distribution of *C. florida* is also outlined showing the isolated subspecies in Mexico. Floristic connections between certain xeromesophytic plants were probably made and broken repeatedly between eastern North America and Mexico during the Pleistocene (Dressler, 1954; Martin and Harrell, 1957). *C. florida* therefore probably had a continuous distribution before and possibly during some parts of the Pleistocene. The presence of *cornivora* in Mexico could furnish clues to the time of origin of this species. Distribution of the host plants is based on Rickett (1944, 1945, 1950).

CINGULATA SPECIES GROUP

Three species and one subspecies of *Rhagoletis* have been found associated with wild and cultivated cherries (*Prunus*): *R. cingulata* (Loew), the eastern cherry fruit fly; *R. cingulata indifferens* Curran, the so-called western subspecies of the cherry fruit fly; and *R. fausta* (Osten Sacken), or black cherry fruit fly are native to North America. The third species, *R. cerasi* (Linn.) is the common European cherry fruit fly and the type of the genus. On the basis of host preference, several authors have referred these three species to the same species group or attested to their close relationship. However, on morphological grounds this is an artificial grouping and does not represent true relationships. As

it is now conceived, the *cingulata* group consists of four native North American species, two associated with the plant genus *Prunus* (Rosaceae) and the other two infesting fruits of *Osmanthus* and *Chionanthus* (Oleaceae). *R. cerasi*⁹ and *R. fausta* are not closely related and should be placed in separate species groups.

Prior to the present revision, these species were generally considered to be only host races or subspecies (Cresson, 1929; Benjamin, 1934; Pickett, 1937; Blanc and Keifer, 1955). Although the species are admittedly very similar, there are several biological reasons for considering them distinct.

In sympatric populations of the *cingulata* group (i.e., *cingulata*, *osmanthi*, and *chionanthi*) consistent morphological differences correlated with host preferences are evident in the dimensions of the ovipositor and wing patterns. These differences could not be maintained in sympatric populations which were not reproductively isolated.

The two allopatric populations associated with the fruits of several *Prunus* species should also be considered distinct. The morphological differences between *indifferens* and *cingulata* are as great or greater than those existing between the sympatric populations of *cingulata* and the two olive-infesting species in Florida. Therefore, there is no reason for considering *indifferens* a subspecies of *cingulata* as it has been in the past.

Diagnosis. The *cingulata* group is easily distinguished from all other *Rhagoletis* species groups on the basis of the following combination of characters: (1) the wing pattern bears a distinct apical fork which may be modified in having the anterior prong of the fork reduced to an apical spot (Figs. 203–204); (2) the surstyli have apical tufts of longer setae (i.e., Figs. 79–82), and the aedeagal tip has a fluted rake-like appendage (Figs. 118–121); (3) the dor-

⁹ For comparative purposes the following morphological features have been illustrated for *R. cerasi*: head (Fig. 39); male genitalia (Figs. 77, 112, 122); spermathecae (Fig. 172); wing pattern (Fig. 211).

sum is dark brown to black and covered by cream to light yellow pollinose microtrichia and decumbent setae arranged in four ill-defined rows; the outer row reaches from just behind the outer scapulars to an imaginary line drawn between the posterior pair of posterior supraalaris; the inner rows reach from the inner scapulars to a point just anterior to the prescutellars.

Certain characteristics of this group suggest a relationship with the *ribicola* group. The spermathecae of members of the *cingulata* group closely resemble those of *ribicola*, while the wing pattern of the latter could be easily derived from that of *cingulata* by simply eliminating the anterior arm of the apical fork. The wing pattern of *berberis* could be derived from that of *cingulata* by eliminating the posterior arm of the fork.

Rhagoletis cingulata (Loew)

Ortalis cerasi. —Harris, 1835, Insects, In Hitchcock, Catalogue of Animals and Plants in Massachusetts, pp. 33–82 (probably refers to *cingulata*).

Trypeta cingulata Loew, 1862, Smithsonian Misc. Coll., 6: 63, 76–77, pl. 2, fig. 11. [Type examined: ♀, "Middle States" (MCZ, No. 13299).]

Trypeta (Rhagoletis) cingulata. —Loew, 1873, Smithsonian Misc. Coll., 8: 263, 329, pl. 10, fig. 11 (notes type from middle states; Long Branch, N.J.).

Rhagoletis cingulata. —Doane, 1898, Ent. News, 9: 69 (in key). —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 15 (in key). —Illingworth, 1912, New York (Cornell) Agr. Expt. Sta. Bull., 325: 191–204 (biology, control, technical description). —Phillips, 1923, J. New York Ent. Soc., 31: 35, fig. 22, pl. 18 (in key, description, wing figured). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 408, pl. 16, fig. 6 (adult taxonomy and redescription). —Curran, 1932, Amer. Mus. Nov., 526: 6, 7 (taxonomy, comparison with *R. indifferens*). —Benjamin, 1934, U.S. Dept. Agr. Tech. Bull., 401: 13–14, 61, fig. 12 (taxonomy, biology of larva and adult). —Pickett, 1937, Canad. J. Res. (D), 15: 60 (genitalia). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 26, 65–66, figs. 22, 67, 122, 123, 169 (larval morphology, in key). —Frick, Sinkover, and Telford, 1954, Washington Agr. Expt. Sta. Tech. Bull., 13: 1–66 (control, biology, intra- and interspecific relationships). —Blanc and

Keifer, 1955, Calif. Dept. Agr. Bull., 44: 77–88, 2 figs. (status of *R. indifferens* and *R. cingulata*).

Diagnosis. The presence of one or more of the following features is usually adequate to distinguish *cingulata* from *indifferens*: (1) an apical ovoid or triangular yellow spot on the posterior margin of tergite V in the male (Fig. 49); (2) an apical fuscous spot on the wing completely separated from the apical band by a hyaline area in most individuals (Table 8); (3) concolorous yellow prothoracic coxa (in *indifferens* black shading is always present on the posterior surface of prothoracic coxa); (4) yellowish orange to light yellow epandrium. No significant differences in the length of the ovipositor or in the length/width ratio, as reported by Blanc and Keifer (1955), were found between these two species.¹⁰

The characters that distinguish *cingulata* from the olive-infesting species in Florida are not as clear-cut. Accurate identification can only be made on a population basis, or on a single specimen if it is accompanied by suitable host data. The following combination of characters may be used to separate Florida populations of *cingulata* from those of *chionanthi* and *osmanthi*: (1) fuscous apical spot present on wing (Table 8); (2) ovipositor length/width ratio averaging 6.0 (4.2–7.9); (3) ovipositor length averaging 0.85 mm (.79–.93) (see Fig. 18); (4) all head and body measurements smaller than olive-infesting species as shown in Tables 9A–9B; (5) larvae infest fruits of black cherry (*Prunus serotina*).

There is apparently little or no overlap in the ovipositor length of *cingulata* and *osmanthi*. There may be considerable difficulty, however, in separating *cingulata* from *chionanthi* without an adequate number of specimens. As a rule, the olive infesting

¹⁰ Mr. Blanc has kindly loaned me the specimens used in making the measurements referred to in the 1955 paper. I obtained the following measurements: *cingulata* 5.8:1, n = 7; *indifferens* 6.1:1, n = 30, as compared with those of Blanc and Keifer: *cingulata* 5.6:1, *indifferens* 7.5:1.

TABLE 8. FREQUENCY OF APICAL WING SPOT IN THE *cingulata* SPECIES GROUP. A SPOT WAS COUNTED ONLY IF IT WAS COMPLETELY SEPARATED FROM THE APICAL CROSSBAND BY A HYALINE AREA. THOSE FORKS WHICH WERE CONSTRICTED AT THE BASE BUT STILL JOINED TO THE APICAL BAND BY A FUSCIOUS REGION WERE COUNTED AS A FORKED PATTERN.

SPECIES	n ♂♂	PER CENT ♂♂ WITH APICAL SPOT	n ♀♀	PER CENT ♀♀ WITH APICAL SPOT
<i>R. cingulata</i> (New York)	95	75.8	48	66.7
<i>R. cingulata</i> (Michigan)	42	71.4	37	59.5
<i>R. cingulata</i> (Penn.)	19	63.2	24	83.3
<i>R. cingulata</i> (Florida)	38	65.8	45	84.4
<i>R. indifferens</i> (all populations)	494	1.4	245	3.2
<i>R. osmanthi</i> (Florida)	26	0	34	0
<i>R. chionanthi</i> (Florida)	12	0	26	0

species are somewhat more yellow than *cingulata*, particularly on the tergites.

Description. Body and wing measurements in Tables 9A–9B. *Head* (Fig. 32): lower two-thirds of postcranium with transverse dark brown stripe, somewhat reduced or absent in specimens from Florida. Frontalia, face, genae, lower two-thirds of postgenae, gulamentum, and mentum yellowish orange; postorbital regions, parafacialia and parafrontalia slightly lighter yellow. Postocellars and genal bristles yellow; gular bristle weak or undifferentiated; all other major bristles black; 8–15 postorbitals. *Thorax*: dorsum covered with white decumbent setae and white pollinose microtrichia arranged in two broad well defined rows, each subdivided into two less distinct rows. Dorsocentrals located on line drawn between anterior supraalars. Normally two pairs pale yellow scapular bristles, both sometimes doubled with supernumeraries

arranged in tandem behind long normal bristles. Pleural and sternopleural bristles brownish black to black, propleuron sometimes tinted with yellow in specimens from southern part of range. Usually only one but sometimes two mesopleural bristles, the second, when present, usually small (24 per cent males and 26 per cent females of all specimens examined had weak to moderately well developed lower mesopleural bristles). Notopleural stripe cream, scutellar spot cream reaching from below apex anteriorly to just before a line drawn between bases of basal scutellar bristles; lateral margins passing through or just outside base of apical scutellars. Postscutellum brownish black to black; halteres lemon yellow. *Legs*: color highly variable. Coxa I, all trochanters, tibiae, and tarsal segments yellowish orange. Femur I usually yellowish orange, sometimes with brownish black tinge along posterior surface; dorsal rows of erect to semierect long bristles yellowish orange, postventral row black. Femur II entirely yellowish orange or with slightly denser black markings on posterior surface than femur I; row of poorly differentiated short black semierect setae on anterior surface of femur II. Femur III mostly yellowish orange or heavily marked with black, particularly along posterior surface. Tibia III with a single row of semierect well developed brown setae on anterior outer surface. *Wing*: pattern variable, Figure 203 representing most frequently encountered condition,¹¹ with upper arm of apical fork broken by hyaline area leaving small apical spot (see Table 8 for frequencies). Figure 204 represents other extreme of pattern with an apical fork. Medial band not joined to basal or subapical bands. Usually single seta dorsally at junction of R_{2+3} and R_{4+5} ; R_{4+5} bare. Anal cell strongly pointed. Crossvein r-m at about midpoint between M_3 and m.

¹¹ Cresson (1929) illustrates the wing of *cingulata* (pl. 16, fig. 6) without a basal crossband. This is undoubtedly an error as I have never seen a specimen of any species in the *cingulata* group which does not bear a conspicuous basal crossband.

	<u>R. cingulata</u> Fla.	<u>R. cingulata</u> N.Y.-Mich.	<u>R. indifferens</u>	<u>R. osmanthi</u>	<u>R. chionanthi</u>
n	10	10	15	10	5
HL	.75±.008 (.72-.79)	.88±.015 (.82-.96)	.82±.015 (.72-.91)	.89±.019 (.78-.96)	.87 (.83-.94)
HW	1.32±.017 (1.23-1.40)	1.47±.018 (1.34-1.54)	1.33±.032 (1.09-1.50)	1.51±.027 (1.34-1.64)	1.50 (1.35-1.67)
HH	1.10±.012 (1.05-1.16)	1.23±.015 (1.13-1.23)	1.09±.029 (.87-1.21)	1.27±.021 (1.19-1.38)	1.27 (1.14-1.41)
LW	.69±.008 (.65-.72)	.75±.010 (.69-.80)	.67±.014 (.55-.73)	.80±.012 (.74-.88)	.73 (.69-.83)
EH	.92±.011 (.86-.95)	1.01±.015 (.90-1.06)	.99±.022 (.72-1.00)	1.05±.018 (.96-1.14)	1.03 (.93-1.13)
FrWV	.43±.005 (.42-.45)	.50±.008 (.44-.53)	.46±.010 (.38-.53)	.46±.009 (.43-.51)	.46 (.40-.53)
AL	.41±.003 (.39-.43)	.46±.002 (.42-.48)	.43±.011 (.35-.53)	.48±.007 (.43-.51)	.45 (.40-.52)
FL	.59±.006 (.56-.61)	.68±.017 (.61-.76)	.60±.013 (.50-.67)	.68±.013 (.62-.75)	.67 (.62-.77)
GW	.16±.003 (.15-.18)	.21±.007 (.18-.25)	.19±.007 (.13-.24)	.22±.008 (.19-.26)	.19 (.17-.22)
TL	1.68±.016 (1.59-1.76)	1.91±.025 (1.76-2.03)	1.68±.040 (1.35-1.90)	1.86±.035 (1.65-1.98)	1.89 (1.70-2.13)
n	10	10	10	10	5
WL	2.78±.021 (2.65-2.88)	3.15±.049 (2.93-3.43)	3.08±.099 (2.61-3.50)	3.06±.065 (2.88-3.34)	3.08 (2.78-3.56)
WW	1.47±.020 (1.37-1.57)	1.65±.041 (1.41-1.83)	1.60±.059 (1.31-1.83)	1.62±.037 (1.34-1.73)	1.71 (1.53-1.93)

Table 9A. Body and wing measurements of males of the cingulata species group. Figures represent mean, standard error, and range.

	<u>R. cingulata</u> Fla.	<u>R. cingulata</u> N.Y.-Mich.	<u>R. indifferens</u>	<u>R. osmanthi</u>	<u>R. chionanthi</u>
n	10	10	15	10	10
HL	.70±.014 (.72-.86)	.92±.017 (.83-.99)	.89±.016 (.72-.97)	.98±.013 (.88-1.03)	.93±.017 (.85-1.00)
HW	1.36±.032 (1.19-1.50)	1.55±.006 (1.44-1.63)	1.48±.030 (1.12-1.60)	1.64±.031 (1.41-1.74)	1.53±.033 (1.31-1.72)
HH	1.10±.021 (1.00-1.19)	1.30±.013 (1.22-1.36)	1.21±.025 (.94-1.33)	1.37±.028 (1.22-1.50)	1.27±.026 (1.15-1.42)
EW	.70±.015 (.61-.76)	.79±.007 (.74-.82)	.75±.013 (.58-.81)	.86±.015 (.75-.92)	.80±.018 (.70-.90)
EH	.93±.022 (.81-1.02)	1.08±.014 (1.00-1.11)	1.00±.023 (.76-1.09)	1.14±.021 (.99-1.21)	1.07±.026 (.95-1.16)
FrWV	.43±.011 (.38-.48)	.54±.008 (.49-.57)	.51±.011 (.39-.57)	.50±.010 (.43-.52)	.47±.015 (.39-.53)
AL	.43±.006 (.41-.45)	.48±.008 (.43-.51)	.46±.011 (.36-.53)	.51±.009 (.45-.56)	.48±.009 (.44-.53)
FL	.61±.017 (.55-.70)	.70±.013 (.62-.75)	.65±.014 (.50-.73)	.74±.016 (.65-.80)	.69±.016 (.61-.78)
GW	.18±.005 (.16-.20)	.22±.002 (.18-.24)	.22±.008 (.15-.26)	.23±.006 (.18-.26)	.21±.009 (.17-.25)
TL	1.81±.046 (1.52-1.98)	2.02±.097 (1.98-2.23)	1.91±.045 (1.39-2.10)	2.09±.048 (1.87-2.26)	1.98±.061 (1.62-2.23)
n	10	10	10	10	10
WL	3.00±.054 (2.75-3.30)	3.62±.021 (3.50-3.76)	3.47±.059 (3.07-3.63)	3.56±.085 (2.84-3.78)	3.31±.072 (2.59-3.67)
WW	1.63±.034 (1.41-1.77)	1.93±.021 (1.90-2.01)	1.82±.034 (1.60-1.93)	1.91±.060 (1.45-2.13)	1.83±.044 (1.64-2.06)

Table 9B. Body and wing measurements of females of the cingulata species group. Figures represent mean, standard error, and range.

Abdomen: variable in color. In northeastern representatives all segments usually black in both sexes with whitish pollinose band of silvery microtrichia along posterior margin of tergites II–IV in male (Fig. 49), and II–V in female as in *indifferens* (Fig. 52); tergite V in male and tergite VI in female with small semicircular yellow mark on posterior margin. Florida specimens with greatly reduced black areas replaced with yellow leaving small irregular brownish black spots on either side of medial line (Fig. 50). *Genitalia: male* — epandrium and surstyli yellowish orange (Figs. 79, 111); genital ring membrane normal; phallic apodeme curved; aedeagus (Fig. 118) with setulose finger-like apical appendage; vesica smooth; ejaculatory apodeme normal (Fig. 152). *Female* — variation in ovipositor length shown in Figure 18; ovipositor tip with two pairs minute preapical setae; ovipositor sheath brownish black to black. Two twisted cylindrical spermathecae covered with small appressed scale-like papillae (Fig. 168); three spermathecal ducts.

Geographical variation. There are three apparent trends of geographical variation in this species. Adult specimens in Florida tend to be smaller than those from the Northeast. Figure 18 illustrates the differences in ovipositor lengths between allopatric and sympatric species in the *cingulata* complex. The second trend is toward a reduction in the black coloration on the abdomen and legs in specimens from the extreme southern parts of the range of *cingulata*. These two tendencies are apparently associated with a shift from a humid to a more xerophytic environment.

There is also a significant difference in the frequency of the apical wing spot between Florida and New York–Michigan specimens (Table 8). The frequency of spotting is considerably higher in females of the Florida population than in those from New York and Michigan.

This may represent a case of character displacement (for details see Brown and Wilson, 1956, and Mayr, 1963). Since the

wing pattern is an important component in courtship displays and species recognition, the presence of a closely related congener may cause the pattern to diverge in the zone of sympatry. *R. cingulata* has no closely related species in the Northeast, and the frequency of the apical wing spot may therefore be less important than in Florida where this species and *chionanthi* are found sympatrically during the same season.

The high frequency of the apical wing spot in *cingulata* females from Pennsylvania indicates that the closely related *chionanthi* may also occur this far north, although no specimens referable to this species have been reported from that area. *Chionanthus americanus*, the host of *chionanthi*, reaches its northernmost limit in southeastern Pennsylvania.

Chromosome number and morphology (Fig. 224). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *Prunus serotina*, Plum Island, Mass., Sept. 10, 1960; Lincoln, New Hampshire, Aug. 27, 1960.

Courtship behavior. The courtship behavior of *cingulata* has not been studied.

Parasites. The only parasite that has been reared from *cingulata* is *Opius ferrugineus* Gahan (Braconidae) (Middlekauff, 1941; Frick et al., 1954). There are probably several other parasites of this species as Frick et al. (1954) have listed nine new ones infesting the sibling species *indifferens* in northwestern United States.

Hosts. A summary of the history leading to the discovery of the hosts of *cingulata* has been presented recently by Frick et al. (1954), and therefore will not be repeated in detail.

The native hosts of this species were not known until about thirty years after it had been first reported as a pest of cultivated cherry. Farleman (1933) found the eastern

cherry fruit fly infesting black cherry, *P. serotina* Ehrh., choke cherry, *P. virginiana* L., and pin cherry, *P. pennsylvanica* L. in Michigan. Glasgow (1933) reported the occurrence of *cingulata* on *P. serotina* in New York, but was unable to rear adults from fruits of either of the other two *Prunus* species even though he frequently observed *cingulata* ovipositing in the fruits of *P. virginiana*. He concluded that *P. virginiana* would only rarely serve as a host for *cingulata*, and could not be regarded as the preferred host for this species in New York. In Massachusetts and New Hampshire, I have never been able to find *cingulata* larvae in *P. virginiana* even when this species was growing among heavily infested *P. serotina*.

I have examined a long series of specimens of *cingulata* from Michigan bearing labels "*P. pennsylvanica*," but it is not clear whether the specimens were reared or simply swept from the tree. Also the identification of the host may be in error. *R. fausta* which normally infests *P. pennsylvanica*, is common in Michigan and it is doubtful that *cingulata* would infest this species of cherry under competitive conditions with *fausta*.

Other hosts of *cingulata* include most of the introduced cultivated cherries such as *P. mahaleb* L. (Mahaleb cherry), *P. avium* (L.) (Mazzard or sweet cherry), and *P. cerasus* L. (sour, Morello, or pie cherry) (Frick et al., 1954).

Distribution (Map 5). *R. cingulata* probably covers most of the range of its principal native host plant, *P. serotina*, in eastern North America. I have never found the fruits of *P. serotina* infested in Mexico, and it is doubtful that *cingulata* occurs south of the Balcones escarpment in Texas.

Rhagoletis indifferens Curran

Rhagoletis cingulata, —Wilson and Lovett, 1913, Oregon Agr. Expt. Sta. Biennial Crop Pest and Hort. Rept., 1911–1912: 160 (first Northwest record of *cingulata*-like species). —Benjamin, 1934 (in part), U.S. Dept. Agr. Tech. Bull., 401: 9, 13, fig. 12, a-1 (synonymy of *indifferens* with *cingulata*). —Pickett, 1937 (in part), Canad. J. Res.

(D), 15: 53–75 (compares genitalic structure of *indifferens* with *cingulata*).

Rhagoletis indifferens Curran, 1932, Amer. Mus. Nov., 526: 6, 8 (on *Prunus emarginata* in Oregon). [Types examined: holotype ♂, Corvallis, Oregon, Aug. 17, 1931 (AMNH); allotype ♀ (same data as holotype); paratypes: Hood River, Oregon, 2 ♂♂, June 12, 1931; 1 ♂, June 23, 1931; 1 ♂, June 1931 (AMNH).]¹² —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 66–67, figs. 24, 69, 127, 171 (larval morphology, in key).

Rhagoletis cingulata indifferens Blanc and Keifer, 1955, Calif. Dept. Agr. Bull., 44: 77–88 (morphological differences between *indifferens* and *cingulata* discussed).

Diagnosis. With the exception of the characters cited below, *indifferens* fits the description of *cingulata*. It may be separated from all other species in the *cingulata* group by the presence of black shading on the posterior surface of coxa I. The epandrium is black instead of yellow as in the three eastern forms. A less useful character for separating *indifferens* from *cingulata* is the almost complete absence of an apical spot in *indifferens* (Table 8; Figs. 203–204). However, on rare occasions an apical spot may occur in *indifferens* (Fig. 205). Generally, *indifferens* is much more heavily pigmented with black than other species in the group. The thorax is always entirely black. The legs, although variable in color, are also more extensively shaded with black. The male abdomen (Fig. 51) lacks yellow shading on the apex of tergite V which is usually present in *cingulata*.

No significant differences in either the ejaculatory apodeme (Fig. 153) or any other structure of the male genitalia (Figs. 81, 107, 119) in sufficiently aged specimens were observed between this species and other members of the *cingulata* group. Such differences were reported by Curran (1932) in his original description of *indifferens*. Body and wing measurements are summarized in Tables 9A–9B; variation in ovipositor length is given in Figure 18.

¹² Curran (1932) states that the type locality of both holotype and allotype is Hood River, Oregon. However, specimens bearing AMNH holotype and allotype labels in Curran's handwriting are from Corvallis, Oregon.

Geographical variation. There is no latitudinal color variation in this species as noted in *cingulata*. The southernmost populations from California are as heavily pigmented as those from British Columbia. There does seem to be a slight trend toward reduction in size in the California specimens, but this tendency is not as great as that noted in the related species, *cingulata*, and in some members of the *pomonella* and *suavis* groups.

Chromosome number and morphology (Fig. 225). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetically chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *P. emarginata*, Dunsuir, California, Aug. 2, 1961; *P. avium*, Corvallis, Oregon, July 20, 1961, and vicinity of Mott Airport, Dunsuir, California, Aug. 12, 1961. Cytological studies on larvae from *P. pennsylvanica* var. *demissa* were not made.

Courtship behavior. The courtship behavior of this species was not studied.

Parasites. Frick et al. (1954) have reared the following hymenopterous parasites from *indifferens*: *Opius ferrugineus* Gahan, *O. rosicola* Muesebeck, *Opius* sp. (Braconidae); *Phygadeuon epochrae* Viereck (Ichneumonidae); *Trybliographa* sp. (Cynipidae); *Tetrastichus faustus* Burks (Eulophidae); *Pachycrepoideus dubius* Ashmead; *Halticoptera* n. sp., *Eupteromalis* sp. near *americanus* Gahan (Pteromalidae); *Psilus* sp. (Diapriidae). Two of these species, *T. faustus* and *P. dubius*, are also parasites of *R. fausta*.

Hosts. The host relationships of *indifferens* have been presented in detail by Frick et al. (1954); therefore only a brief summary will be given here with the addition of references appearing since 1954.

The first report of *indifferens* in cultivated cherries (*P. avium* L.) growing in Oregon was made by Wilson and Lovett

(1913) about 89 years after the introduction of the first cherry seedlings into the Northwest (Jones, 1963, *in litt.*). The native host of this species, *Prunus emarginata* (Dougl.) D. Dietr. (wild pin cherry), was first reported by Keifer (1938), and later Frick et al. (1954) added *P. virginiana* L. var. *demissa* (Nutt.) Torr. to the host list. Recently two more *Prunus* species have been found to be hosts of the western cherry fruit fly. Ellertson (1961) reported larvae of *indifferens* infesting the fruits of *P. subcordata* Benth (Pacific plum) near The Dalles in Oregon, and the introduced *P. salicina* Lindl. (Japanese plum) at Hood River, Oregon. This is the first record of a member of the *cingulata* group infesting plums.

Distribution (Map 5). *R. indifferens* does not reach as far south or as far north as its principal host, *P. emarginata*. Its presence in Montana beyond the range of this wild cherry represents recent introduction of *indifferens* into commercial cherry growing areas.

Rhagoletis osmanthi new species

Types. Holotype ♂, Osceola Co., Florida, larva collected Nov. 13, 1929, emerged Oct. 18, 1930, ex *Osmanthus americanus* (Slight) (USNM, No. 67376); paratypes: 3 ♂♂ 5 ♀♀, Alligator Lake, Osceola Co., fruit collected Nov. 13, 1929, ex *O. americanus* (Slight) (USNM).

This species and the one following are being described from material reared during the 1929–1933 Mediterranean fruit fly campaign in Florida where extensive collections of native fruit flies were made on a wide variety of host plants. The taxonomic results of these investigations were summarized in a publication by Benjamin (1934), and the biology in an unpublished but extremely useful report by Nicholson (1929–30).

Benjamin noted that specimens reared from cultivated cherries (probably from the Northeast as cultivated cherries are not grown in Florida) and material from



Florida associated with the fruits of wild tea-olive and fringe trees (Oleaceae) were larger than those reared from native Florida wild cherry, *Prunus serotina*. He did not consider these differences worthy of further recognition. It is evident, however, that the populations associated with wild olives in Florida represent two very closely related sibling species.

Diagnosis. *R. osmanthi* can be distinguished from *cingulata* in Florida by the following combination of characters: (1) the presence of a forked apical wing band; (2) a longer ovipositor (for comparison with *cingulata*, see Fig. 18); (3) considerably larger size (Tables 9A–9B); (4) *osmanthi* infests only the fruits of *Osmanthus* spp.

It is more difficult to differentiate *osmanthi* from the other olive infesting species, *chionanthi*, as both have a forked apical wing band. The latter species is distinctly smaller than *osmanthi* (Tables 9A–9B; Fig. 18), although some overlap in both sexes does occur. Rearing records also indicate that these fly populations are allochronically isolated with their emergence synchronized with the maturation of their respective host fruits (see *Hosts*). Adults of *R. osmanthi* occur in the winter months between October and January, while *chionanthi* is active only in the summer from mid-July to early August.

The only useful character for separating these species is the difference in ovipositor length. But even this may not be reliable when host data is lacking and only one specimen is being considered as it may fall within the range of *chionanthi*. On a population basis, however, the ovipositor length between these two species is significantly different at the .05 level using the standard t-test ($t_{18, .05} = 2.10 < 4.07$ ∴ reject H_0). Thorax length may be used to distinguish males (see Table 9A), although the variation in this character is somewhat higher than ovipositor length.

In all other respects *osmanthi* fits the description of *cingulata*. Figures of the wing

(206), abdomen (53–54), and male genitalia (82, 108, 120, 155) are included for comparative purposes. Body and wing measurements may be found in Tables 9A–9B.

It should be stressed that *osmanthi*, as well as the closely related *chionanthi*, is much more extensively marked with yellow than the northeastern population of *cingulata*. However, it is impossible to differentiate between the Florida representatives of *cingulata*, *osmanthi*, and *chionanthi* as they have similar color patterns.

There is never a trace of black or dark brown maculation on the postcranial regions or on any segments of the legs in *osmanthi*, and there are also extensive areas of yellow on the pleural regions and on the tergites of the abdomen.

Chromosome number and morphology. The chromosomes of this species have not been studied.

Hosts. *R. osmanthi* has been reared only from *Osmanthus americanus* (L.) Gray (wild tea-olive, devilwood) growing in Florida. *Osmanthus* (Oleaceae) is a genus of more than 30 species primarily of eastern and northeastern Asia with only two to four species represented in North America (Wilson and Wood, 1959). At least three allopatric variants have been described from peninsular Florida, some of which are recognized as distinct species. It is not known if *R. osmanthi* infests all these forms, but considering the oligophagous nature in host specificity recorded for other *Rhagoletis* species, it is reasonable to assume that it does.

O. americanus occurs from central Florida north along the coastal plain to southeastern Virginia, and west to southeastern Louisiana (see Map 6). Isolated populations of this species also occur in Nuevo Leon, Oaxaca, and Vera Cruz, Mexico, with a second species, *O. mexicanus* Lundell, known from a single locality in Chiapas, Mexico (Green, 1958; Wilson and Wood, 1959). *R. osmanthi* may therefore cover a wider range than its present Florida



records indicate. Collection and rearing data suggest that *osmanthi* is common on its host fruit from October through January. Nicholson (1929-30) reports that flies emerge following a nine- to eleven-month diapause from mid-September to mid-March. This emergence closely corresponds to the maturation time of the host fruit and as yet is not known to overlap the emergence periods of the closely related species *chionanthi* (mid-July to early August).

Distribution (Map 6). The species has been recorded in the following Florida localities: De Leon Springs, Coronado Beach, Volusia Co.; Alligator Lake and 7 mi. E Kissimmee, Osceola Co.; Seffner, Thonotosassa, Hillsborough Co.; Tarpon Springs, Pinellas Co.; New Port Richey, Pasco Co.

Rhagoletis chionanthi new species

Types. Holotype ♀, Apopka, Florida, larva collected Sept. 12, 1929, emerged June 13, 1930, ex *Chionanthus virginicus* (W. S. Earle) (USNM No. 67377); paratypes: 3♂♂ 6♀♀, 6 mi. SW Kissimmee, Florida, July 1930, ex *C. virginicus* (G. F. Harding) (USNM).

Diagnosis. The characters separating *chionanthi* from the closely related species *osmanthi* are (1) a mean difference in ovipositor length (Fig. 18), and (2) a difference in host preference and emergence period. The emergence is synchronized to coincide with the ripening of the fruits of *C. virginicus*. No entirely suitable method has been found to separate the males of the two olive infesting species, although thorax length may tentatively serve to identify some specimens. For a detailed discussion of the differences between these two species, see the diagnosis of *osmanthi*.

In all other respects *chionanthi* fits the description of *cingulata*. Figures of the wing (207), abdomen (55-56), and male genitalia (80, 109, 121, 154) are included for comparative purposes. Body and wing measurements may be found in Tables 9A-

9B. For the variation in ovipositor length consult Figure 18.

As in the case of *osmanthi*, *chionanthi* can be easily distinguished from north-eastern representatives of *cingulata* on the basis of color pattern. The similarities between these three species in Florida make it impossible to separate them on the basis of color alone.

Chromosome number and morphology. A cytological study of this species was not made.

Hosts. Nicholson (1929-30) reared this species from *Chionanthus virginicus* L. (fringe-tree or old man's beard) (Oleaceae). This small genus of plants is represented by three or four species, two in eastern North America and one or two in eastern Asia. *C. virginicus* ranges from Florida to Texas northward to New Jersey, Pennsylvania, West Virginia, southern Ohio, southern Missouri, and Oklahoma (see Map 6). A second species, *C. pygmaeus* Small is endemic of the sandscrub of the lake region of central Florida (Wilson and Wood, 1959) and may also be infested by *chionanthi*. As in the closely related species, *R. osmanthi*, *chionanthi* probably has a much wider distribution than indicated by the specimens available for study.

Nicholson reports that this species is active from mid-July to early August.

Distribution (Map 6). *R. chionanthi* has been recorded from Satalah, Rabun Co., Georgia, and the following Florida localities: Apopka and Wakiwa Springs, Orange Co.; vicinity of Kissimmee, Osceola Co.; St. Augustine, St. Johns Co.; Lake Juliana, Auburndale, Polk Co.

SUAVIS SPECIES GROUP¹³

The members of the *suavis* group are of particular interest in that they provide a completely different picture of speciation from that of the *pomonella* and *cingulata*

¹³ Benjamin (1934) referred to this complex as the *juglandis* group. I have chosen to follow Cresson (1929) who originally established the group to include all the walnut infesting species.

groups. The predominance of allotrophic sibling species is the outstanding feature of the latter two groups where a wide range of host families and genera have been adopted in the course of speciation. These drastic shifts in hosts have been accompanied by only slight morphological changes. Members of the *suavis* group, on the other hand, are syntrophic as they are capable of infesting only species within the genus *Juglans* (Juglandaceae) (Boyce, 1934; Christenson and Foote, 1960). Unlike the *pomonella* and *cingulata* complexes, the walnut infesting species have developed a wide range of morphological differences, particularly in size and body coloration. These differences are so distinct that it is possible to recognize each species without microscopic examination.

Diagnosis. The *suavis* species group may be distinguished from others in the genus *Rhagoletis* by the following combination of characters: (1) males have a well developed pouch-like invagination located in the membrane between the genital ring and fultella (Fig. 75, GRMP); (2) the scutellum is concolorous cream to light yellowish orange without a distinct spot as in most other *Rhagoletis* species; (3) the setae and microtrichia covering the dorsum do not form a pattern of vertical stripes but present a homogeneous appearance; (4) the larvae normally feed in the husks of various *Juglans* species.

Sexual dimorphism in color patterns of the thorax and abdomen are present in *completa*, *zoqui*, and to a lesser extent, *suavis*. Males of *completa* and *zoqui* have more extensive black markings on the legs, pleural regions of the thorax, and abdominal tergites than do the females. The variation in color pattern between the sexes of *suavis* is limited to the abdominal tergites. The degree of coloration in the three species varies considerably among individuals with some heavily colored females approaching the color of lightly pigmented males.

The chromosome number ($n=12$) and

morphology are identical in all species, with five metakinetinetic and two small acrokinetic dot chromosomes. No heteromorphic sex chromosomes were noted.

Rhagoletis suavis (Loew)

Trypeta suavis Loew, 1862, Smithson. Misc. Coll., 6: 63, 75, pl. 2, fig. 10. [Type examined: sex unknown (only wings and part of dorsum remain of this specimen), "Middle States" (MCZ, No. 13293).]

Acida suavis, —Osten Sacken, 1878, Smithson. Misc. Coll., 16: 189 (notes type in MCZ).

Rhagoletis suavis, —Coquillett, 1899, J. New York Ent. Soc., 7: 260 (new status). —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 7, 14 (description, in key, hosts). —Phillips, 1923, J. New York Ent. Soc., 31: 135–136, pl. 18, fig. 24 (in key, host). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 411–412 (in key, redescription). —Boyce, 1934, Hilgardia, 8: 375–376, figs. 4, 12, 13 (biology, description, interspecific relationships). —Pickett, 1937, Canad. J. Res. (D), 15: 61, fig. 11 (genitalia, compared with *completa*). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 26, 74–76, figs. 30, 75, 136, 137, 177 (larval description, in key).

Diagnosis. The wing pattern of *suavis* may be used to separate this species from its closest relative, *completa*. The medial and subapical bands in *suavis* are normally joined by a broad fuscous band extending diagonally across M_{1+2} between r-m and m (Fig. 190). In some specimens this band may be broadened to cover most of the region in the discal cell between r-m and m (Fig. 191). Specimens of *completa* may have the medial and subapical crossbands joined by a narrow fuscous bridge at right angles to the two crossbands at various points in the regions of cell 1st M_2 (discal cell), as illustrated in Figure 193, and by Foote and Blanc (1963, Fig. 73). This pattern is readily distinguished from that of *R. suavis* in that it is never diagonal to the long axis of the wing. The medial band is also much wider in *suavis* than in *completa*. The presence of a concolorous yellow postscutellum in both sexes of *suavis* may also be used to distinguish this species from *completa* which has this region either marked by two broad vertical brown bands or is concolorous brown.

In a study of the genitalia of these two species, Pickett (1937) found no distinct differences in the tip of the aedeagus or in the surstyli. He thus concluded that the genitalia are of no use in distinguishing between *suavis* and *completa*. However, I have found that the genitalia do offer the following useful characters. The tip of the aedeagus in *suavis* bears a setulose finger-like appendage (Fig. 129), while in *completa* the tip is modified to form a rake-like fluted appendage (Fig. 131). Also, the vesica of the latter species is bifurcate, while in *suavis* it is entire. Boyce (1934) noted that the surstyli of *completa* when viewed mesolaterally are somewhat curved and taper gradually from the region of the prensisetae toward the distal end, while those of *suavis* are only very slightly curved and taper abruptly at the distal end. Pickett (1937) correctly pointed out that in order to get the surstyli to appear like those in Boyce's figure, it is necessary to orient the epandrium so that a posterior lateral view is obtained. Nevertheless, there are slight but consistent differences between the surstyli of the two species, although not as obvious as figured by Boyce. The surstyli of *suavis* are slightly thicker in the region of the prensisetae and therefore less curved in appearance than those of *completa* (Figs. 73, 75). The structure of the ejaculatory apodeme was also used by Boyce to separate these two species, but as already pointed out by both Pickett (1937) and myself, this structure is of little use in differentiating most members of the genus *Rhagoletis*.

Description. Body and wing measurements in Tables 10A–10B. *Head* (Fig. 30): mentum, postcranial, postgenal, and gular regions golden yellow with postorbital region light golden yellow to cream; frontalia, parafrontalia, parafacialia and genae yellowish orange; face tannish cream. Occipital, postvertical (0-2), postorbital (7-15), genal, and well developed gular bristles golden yellow to yellowish orange; all other major bristles black. No black or

brown markings on head. *Thorax*: dorsum golden yellow, covered evenly with decumbent golden yellow setae and silvery white to golden yellow pollinose microtrichia. Dorsocentrals slightly behind anterior supraalars. Pleural and sternopleural regions golden yellow without distinct black markings in either male or female. Propleural bristles light yellow; two mesopleural bristles of about equal size. Notopleural stripe cream to white; dorsum of scutellum cream at apex, grading to golden yellow at base. Postscutellum and halteres concolorous golden yellow. *Legs*: all segments golden yellow. Dorsal rows of erect to semierect long bristles in femur I golden yellow, postventral row black. A row of semierect golden yellow short bristles along anterior surface of tibia II, well differentiated from shorter decumbent setae. Tibia III with row of weakly differentiated stout semierect golden yellow setae on anterior outer surface. *Wing*: Normal wing pattern as in Figure 190, with Figure 191 representing an extreme in variation of pattern. In all specimens thus far examined medial band always joined to subapical band by a diagonal fuscous band crossing M_{1+2} between crossveins r-m and m. Some individuals may have fuscous area joining these two bands broadened, reaching from M_{1+2} almost to posterior margin of wing. Medial band not joined to basal band and ending in cell Cu_1 . *Abdomen*: base color of all tergites golden yellow to dark yellowish orange; tergites I–III of male (Fig. 59) and I–IV of female (Fig. 60) bearing pollinose cream colored band along posterior margin; tergites of male usually progressively more heavily shaded with black markings from basal segments to apex. *Genitalia: male*—epandrium (Figs. 75, 99) yellowish orange to dark brown with surstyli yellowish orange to golden yellow; aedeagus (Fig. 129) with finger-like appendage covered with short setae at tip, resembling that of *juglandis* (Fig. 130); vesica smooth, unforked; genital ring pouch well developed (Fig. 75, GRMP); phallic apodeme

	<u>R. suavis</u>	<u>R. completa</u>	<u>R. juglandis</u>	<u>R. boycei</u>	<u>R. zoqui</u>
n	17	14	10	10	10
HL	1.06±.036 (.81-1.30)	1.06±.030 (.88-1.23)	.91±.031 (.79-1.06)	.97±.045 (.79-1.32)	1.19±.026 (1.08-1.30)
HW	1.63±.051 (1.34-1.90)	1.59±.046 (1.31-1.81)	1.37±.041 (1.22-1.53)	1.39±.064 (1.14-1.79)	1.76±.041 (1.58-1.94)
HH	1.41±.037 (1.12-1.61)	1.33±.040 (1.11-1.51)	1.11±.037 (.96-1.28)	1.17±.052 (1.00-1.55)	1.52±.044 (1.31-1.70)
EW	.82±.018 (.73+.91)	.80±.020 (.69+.91)	.71±.025 (.60-.80)	.68±.032 (.56-.88)	.88±.016 (.82-.95)
EH	1.13±.028 (.88-1.29)	1.09±.034 (.88-1.26)	.91±.032 (.76-1.04)	.97±.048 (.80-1.29)	1.24±.028 (1.13-1.38)
FrWV	.59±.018 (.48-.71)	.54±.018 (.41-.62)	.31±.016 (.44-.58)	.50±.021 (.40-.61)	.55±.017 (.47-.62)
AL	.53±.011 (.44-.60)	.53±.016 (.44-.60)	.43±.011 (.39-.49)	.48±.023 (.39-.60)	.60±.012 (.55-.65)
FL	.79±.033 (.55-.95)	.78±.026 (.63-.92)	.67±.025 (.37-.80)	.68±.041 (.55-.95)	.88±.024 (.79-1.00)
GW	.28±.021 (.21-.36)	.26±.011 (.20-.32)	.21±.001 (.17-.24)	.20±.013 (.16-.30)	.28±.013 (.21-.35)
TL	2.60±.045 (2.14-3.08)	2.24±.071 (1.77-2.59)	1.85±.064 (1.57-2.10)	2.13±.070 (1.66-2.97)	2.72±.068 (2.41-3.06)
	15	18	10	10	10
WL	4.57±.099 (3.83-4.97)	3.76±.104 (2.75-4.32)	3.41±.129 (2.94-3.99)	4.30±.171 (3.53-5.30)	4.71±.161 (3.99-5.53)
WW	2.22±.049 (1.86-2.45)	1.90±.060 (1.31-2.29)	1.62±.064 (1.41-1.96)	1.93±.078 (1.60-2.45)	2.29±.074 (1.93-2.61)

Table 10A. Body and wing measurements of males of the suavis species group. Figures represent mean, standard error, and range.

	<u>R. suavis</u>	<u>R. completa</u>	<u>R. juglandis</u>	<u>R. boycei</u>	<u>R. zoqui</u>
n	15	14	10	10	10
HL	1.09±.026 (.83-1.21)	1.06±.038 (.71-1.21)	.94±.031 (.83-1.04)	.96±.024 (.84-1.08)	1.17±.019 (1.06-1.24)
HW	1.65±.031 (1.38-1.82)	1.56±.045 (1.17-1.78)	1.41±.047 (1.20-1.63)	1.42±.048 (1.22-1.54)	1.79±.027 (1.62-1.90)
HH	1.31±.010 (1.18-1.57)	1.29±.043 (.92-1.44)	1.15±.043 (.95-1.34)	1.18±.031 (1.00-1.31)	1.52±.025 (1.37-1.63)
EW	.82±.015 (.70-.89)	.79±.026 (.54-.92)	.71±.022 (.60-.78)	.71±.017 (.62-.78)	.90±.001 (.84-.95)
EH	1.13±.026 (.95-1.28)	1.07±.029 (.72-1.21)	.92±.032 (.80-1.07)	.98±.026 (.85-1.08)	1.27±.022 (1.13-1.35)
FrWV	.59±.019 (.45-.68)	.54±.020 (.37-.65)	.55±.026 (.41-.68)	.48±.018 (.36-.55)	.52±.001 (.46-.56)
AL	.54±.012 (.46-.62)	.51±.018 (.35-.60)	.44±.014 (.38-.52)	.49±.011 (.43-.54)	.61±.011 (.54-.66)
FL	.79±.020 (.64-.87)	.77±.030 (.49-.90)	.70±.026 (.57-.81)	.69±.018 (.59-.75)	.87±.017 (.75-.95)
GW	.28±.010 (.18-.34)	.26±.013 (.16-.32)	.23±.013 (.17-.30)	.20±.007 (.15-.22)	.28±.001 (.22-.31)
TL	2.54±.071 (2.06-2.86)	2.22±.069 (1.43-2.63)	1.94±.077 (1.57-2.30)	2.13±.072 (1.78-2.56)	2.71±.045 (2.52-2.85)
	15	18	10	10	10
WL	4.57±.122 (3.86-5.36)	3.76±.095 (3.11-4.28)	3.70±.098 (3.24-4.12)	4.30±.050 (3.73-4.68)	4.91±.088 (4.45-5.36)
WW	2.25±.060 (1.86-2.55)	1.91±.052 (1.50-2.19)	1.70±.082 (1.54-2.03)	2.00±.046 (1.77-2.26)	2.46±.035 (2.29-2.68)

Table 10B. Body and wing measurements of females of the suavis species group. Figures represent mean, standard error, and range.

straight or only slightly bent. Ejaculatory apodeme normal (Fig. 141). *Female*—variation in ovipositor length (Fig. 20); ovipositor sheath yellowish orange to chestnut brown; three cylindrical spermathecae with very small appressed scale-like papillae (Fig. 157); ovipositor tip with two pairs minute preapical setae.

Geographical variation. There is no evidence of geographical variation in the morphology or in wing and body color patterns of this species. Adult size seems to vary considerably within a given region, a feature common to all members of this species group. The apparent reason for this size variation may be mainly a nutritional one. Crowding occurs frequently as females oviposit readily in the same walnut (Boyce, 1934); the husk may therefore be consumed before the larvae are fully mature. In the material examined there was no apparent tendency for the adults to become progressively smaller toward the southern distributional limits, a characteristic of the related species, *completa*, and certain members of other species groups (i.e., *cingulata* and *pomonella*).

Chromosome number and morphology (Figs. 218–219). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *Juglans cinerea*, Cambridge, Mass., 8 Sept. 1960; *J. nigra*, Pemberton, New Jersey, 15 Oct. 1961.

Courtship behavior. Courtship has been described by Brooks (1921) and is similar to that reported for *completa* by Boyce (1934).

Single males set up and defend temporary territories on nuts suitable for oviposition. Walnuts are preferred which show some mechanical damage to the husk in which the female can readily oviposit. The males remain for hours on this site where

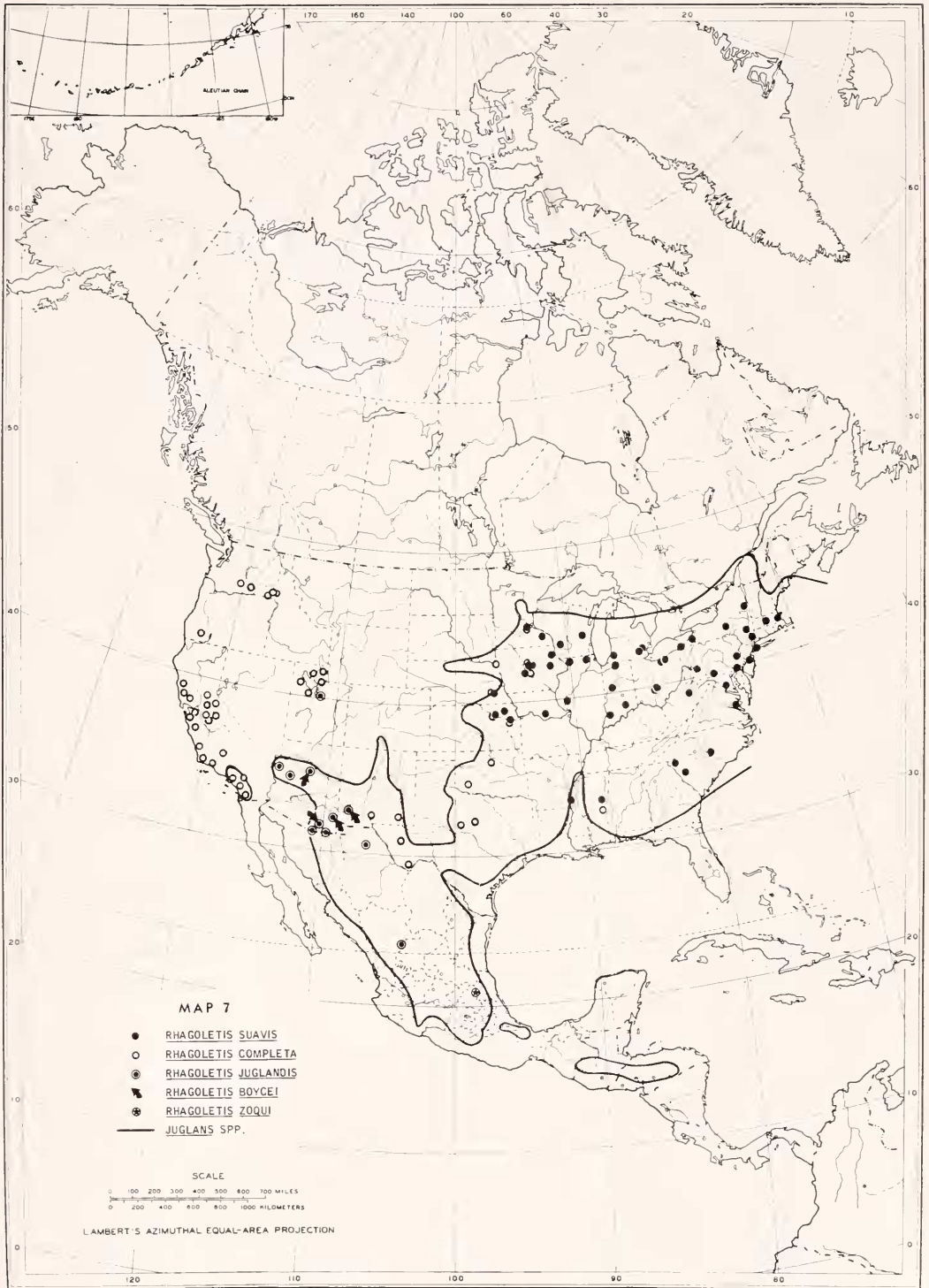
they patrol in short turning movements about the nut. When another male alights on the nut, the original occupant attacks with lunging movements, the wings at first held vertically above the thorax followed by wing waving. If the resident male fails to dislodge the new arrival, the pair will enter into a "boxing match," both reared on their hind legs, striking and grappling with their fore legs. Usually the original occupant succeeds in driving off the other male or both fall off the nut and only one (presumably the resident male) returns, whereupon he begins once again to patrol the nut.

Brooks described the approach of the female as slow and deliberate, taken in stages of flying and crawling on leaves and twigs near the nut before alighting on it. When the male observes the approaching female, he becomes excited and rapidly moves back and forth, whirling around and raising and lowering his wings with the white spot and dark body in sharp contrast to the green walnut husk.

On the arrival of the female, the male backs away from the oviposition site and remains stationary with wings elevated above the back while facing the female. When the female attempts to oviposit, the male usually springs upon her and copulation takes place. This is often followed by alternate periods (4–5) of egg laying and copulation, the male sometimes remaining mounted and sometimes dismounting. After the female has left, the male frequently remains on guard and resumes his patrolling.

There appears to be a strong tendency for flies to congregate only in certain trees and on the lower branches. Feeding on the exudates emanating from oviposition sites has been observed many times.

Parasites. Babb (1902) reared *Aphaereta auripes* Provancher (Hymenoptera, Alysidae) from larvae collected at Amherst, Mass. No other parasites have been described from this species, nor have I been



able to rear parasites from walnuts collected at five widely separated localities.

Hosts. This species has been reared only from the husks of *Juglans* species. A single report by Stirrett (1936) that *suavis* occurs also in hickory nuts (*Carya*, Juglandaceae) should be accepted with some caution. No *Rhagoletis* has actually been reared from *Carya* by any investigator. Stirrett merely states that local growers of commercial walnuts had reported *suavis* mining in the husks of local hickory nuts, but he did not confirm this observation through rearing. It is sometimes easy for the untrained observer to confuse a fly maggot with a lepidopterous larva, as Biederman probably did when he described the larva of *juglandis* descending from a walnut to the ground on a thread (Cresson, 1920).

Larvae of *suavis* have been reared from the following host plants: *Juglans nigra* L. (black walnut) (Babb, 1902, and others); *J. cinerea* L. (butternut) (Banks, 1912, and others); *J. regia* L. (Persian or English walnut, native to western Europe and Asia) (Brooks, 1921, and others); *J. Sieboldiana* Maxim. (native to Japan) (Brooks, 1921).

Distribution. As illustrated in Map 7, *suavis* covers the eastern two-thirds of the range of *J. nigra* and probably the entire range of *J. cinerea*. Records of *suavis* from Oklahoma and Texas are lacking and in these regions *completa* seems to be the only species on *J. nigra*.

Rhagoletis completa Cresson

Rhagoletis suavis completa Cresson, 1929, Trans. Amer. Ent. Soc., 55: 412, pl. 16, fig. 9. [Type examined: ♂, Chino, San Bernardino Co., Calif., Aug. 10, 1928, Persian walnut (A. M. Boyce) (ANSP, No. 6364); paratypes examined: 2 ♀♀, same data as type; 1 ♀, Chino, Calif., Aug. 15, 1929 (A. M. Boyce) (ANSP, No. 6341; MCZ, No. 19467); 1 ♀, Pomona, Los Angeles Co., Calif., Aug. 10, 1929 (A. M. Boyce) (ANSP, No. 6364).] —Pickett, 1937, Canad. J. Res. (D), 15: 61 (genitalia, status).

Rhagoletis completa, —Boyce, 1931, J. Econ. Ent., 24: 1018–1024 (diapause). —Curran, 1932, Amer. Mus. Nov., 526: 6. —Boyce, 1934, Hilgardia, 8: 361–379 (bionomics, control).

—Phillips, 1946, Mem. Amer. Ent. Soc., 12: 27, 64–65, figs. 31, 76, 138, 139, 178 (larval morphology, in key).

Diagnosis. In general appearance similar to *suavis*, but smaller and displaying more marked sexual dimorphism in body coloration. The differences in the wing pattern, body markings, and aedeagal morphology make it easy to differentiate this species from *suavis*, its closest relative. For a discussion of these differences, see the diagnosis of *suavis*.

Description. Body and wing measurements in Tables 10A–10B. Male and female about same size. *Head* (Fig. 28): entirely yellow. Postcranial region light yellowish orange; postorbital region light yellow; frontalia golden yellow, parafrontalia slightly lighter; parafacialia light yellow, in distinct contrast with golden yellow face; genae light yellowish orange grading to white posteriorly; postgenal regions and gulamentum white with faint tint of yellow; mentum light brown. Genal, occipital, postvertical, postorbital (7–12), and strong gular bristles yellow to yellowish orange; all other major bristles black. *Thorax: male*—dorsum concolorous tawny to raw sienna, uniformly covered with light yellow to golden yellow decumbent setae and microtrichia, without vertical banded pattern. Propleural bristles light yellow; all other major bristles black. Two mesopleural bristles of about equal size. Pleural and sternopleural regions brownish black. Notopleural stripe light yellow; scutellum light yellow grading to deeper golden yellow at base; halteres golden yellow. Base color of postscutellum golden yellow with two broad vertical brownish black bands; some specimens with postscutellum concolorous brownish black. *Female*—dorsum, humeral stripe, and scutellum as in male. Pleural and sternopleural regions lighter with variable brownish black markings on pleural regions, rarely slight brownish black markings on dorsal margin of sternopleuron. Vertical stripes present on postscutellum but frequently much narrower than in

male. *Legs: male*—coloration highly variable. Coxae I and II generally brownish black; coxa III golden yellow. Trochanters golden yellow to tan. Femur I brownish black with dorsal rows of bristles golden yellow to brownish black; ventral row black. Femur II tan with single row of weak semierect stout setae on anterior surface. Femur III golden yellow or tan grading to brownish black ventrally. Fifth and occasionally part of fourth tarsal segment on each leg dark brownish yellow, remaining segments tan to golden yellow. Tibiae I and II straw colored. Tibia III golden yellow grading to brownish black ventrally; outer surface with single row of about eight yellowish orange semierect setae. *Female*—all leg segments golden yellow without black markings; last tarsal segment sometimes dark yellowish brown. All setae and bristles as in male. *Wing* (Figs. 192–193): pattern convergent with that of *R. berberis* (Fig. 202) to which *completa* apparently bears no close relationship. Medial band rarely joined to subapical band; if joined then only narrow fuscated bridge at right angles to two crossbands present and never angled as in *suavis* (Fig. 190); medial band not joined to basal band. Junction of R_{2+3} and R_{4+5} with 0 to 2 setae dorsally, 0 to 2 ventrally; R_{4+5} bare. Anal cell strongly pointed with r-m about midway between crossveins M_3 and m. *Abdomen: male* (Fig. 63)—coloration highly variable. Normally tergites I and II golden yellow with some brownish black shading on either side of medial line. Tergites III–V generally golden yellow but becoming progressively more heavily marked with brownish black; tergite V usually almost entirely brownish black. Tergites II, III, and IV with pollinose cream colored band along posterior margin. *Female* (Fig. 64)—as in male, coloration variable, but all segments substantially more golden yellow than male. Tergites III–V usually marked with some dark shading on either side of medial line and with cream colored pollinose band along posterior margin of tergites III–VI.

Genitalia: male—epandrium and surstyli golden yellow (Figs. 73, 97), surstyli somewhat narrower than those of *suavis* (Figs. 75, 100); aedeagus with fluted, rake-shaped apical appendage (Fig. 131); genital ring pouch well developed; phallic apodeme straight. Ejaculatory apodeme normal (Fig. 145). *Female*—variation in ovipositor length shown in Figure 20; ovipositor sheath golden yellow to brown; three cylindrical spermathecae with very small appressed, scale-like papillae (Fig. 158), similar to those found in *suavis* except narrower (Fig. 157); ovipositor with two pairs of minute preapical setae.

Geographical variation. There is a marked trend toward reduction in size in specimens from the Southwest (Texas and New Mexico). Not enough material was available for a statistical analysis. This tendency has also been noted in *pomonella* and *cingulata*, and apparently is correlated with a shift to a more arid habitat. A series of specimens from Lincoln, Nebraska, are also considerably smaller than those from the neighboring states of Minnesota, Iowa, and Kansas (see Fig. 20 for comparison of ovipositor length). These specimens are all teneral indicating that they were probably reared and killed before they had attained full coloration. The reason for their small size is not known, but they may have emerged from overcrowded conditions as they all resulted from a single collection of walnuts.

Chromosome number and morphology (Fig. 220). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *J. regia*, Anaheim, California, 15 Aug. 1961; *J. californica*, Riverside, California, 15 Aug. 1961.

Courtship behavior. The courtship behavior of *completa* is similar to that of *suavis* and has been briefly outlined by

Boyce (1934). Males are territorial and usually begin patrolling walnuts in the late afternoon when mating is most frequently observed. Resident males recognize and attack any male or other insect that lands on the walnut. In aggressive display, the wings are held vertically above the thorax. This display is used in the preliminaries of courtship by *suavis*. The resident male attempts to repel the intruder by rushing and butting. If this fails to dislodge the intruder, then a "boxing match" may follow, with both flies standing on their hind legs venter to venter, striking each other with the fore and middle legs. Aggressive displays and fighting may last as long as two to three minutes before one of the males flies away.

The male reacts very differently to the female when she lands on the walnut. His movements become more rapid and excited. Facing the female and moving sideways, he attempts to circle her; she will either ignore the male and begin ovipositing or fly away. As soon as oviposition is completed, the male mounts. In *suavis*, mating may occur before oviposition. As the male mounts, the female spreads her wings laterally, raises her abdomen and extrudes the ovipositor which the male grasps with the surstyli. Mating in the field lasts from two to fifteen minutes.

Parasites. Two apparently general-feeding parasites of dipterous pupae have been reared from *completa*. These are *Spalangia rugosicollis* Ashmead (Chalcididae), and *Salesus* sp. (Proctotrypoidea) very near *atricornis* Ashmead (Boyce, 1934). Boyce also reports that a larval parasite, *Opius humilis* Silvestri (Braconidae), introduced from Hawaii was successfully established in California on *R. completa*.

Hosts. *R. completa* has been reared from *Juglans nigra*, a species which is native to eastern North America but falls within the normal range of *completa* in Minnesota, Iowa, and the eastern part of Kansas, Oklahoma, and Texas (Boyce, 1934, and others).

Soon after the introduction of *completa*

into California, sometime between 1922 and 1925, *J. californica* S. Watson (California black walnut), a species restricted to coastal southern California (Santa Barbara Co. to Orange Co.), and *J. hindsii* Rehd.¹⁴ (Hinds black walnut), which ranges farther north along the east slopes of the Napa range to Walnut and Lafayette creeks, Contra Costa Co., were reported to be hosts of *completa* (Boyce, 1929, 1934).

The occurrence of *completa* in peaches (*Prunus persica* (L.) Batsch) in Utah (Anonymous, 1962) and California (Anonymous, 1964) is not surprising. The peach, as already mentioned, appears to be highly susceptible to fruit fly attack under certain conditions.

Distribution (Map 7). The distribution of *R. completa* reaches its most northeastern limit in southern Minnesota. It ranges southward along the transition zone, in sympatry with *R. suavis*, to Texas and possibly northern Mexico, and westward to central New Mexico. I have also seen one unlabeled specimen of *completa* from Mississippi, indicating that the species may extend its range farther eastward in the southern limits of its range than it does in the north.

Rhagoletis juglandis Cresson

Rhagoletis juglandis Cresson, 1920, Ent. News, 31: 65-66. [Holotype examined: ♂, Carr Canyon, Huachuca Mts., Ariz., July-Aug., 1919 (C. R. Biederman) (ANSP, No. 6235); paratypes examined: 11 ♂♂, same data as holotype.] —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 413, pl. 16, fig. 11 (redescription, in key). —Boyce, 1934, Hilgardia, 8: 376-377, figs. 4C, 13, 14 (redescription, notes on biology). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 27, 67-68, figs. 25, 70, 128, 172 (larval morphology, in key).

Diagnosis. *R. juglandis* is easily recognized by its entirely light yellow coloring, complete absence of body markings, and

¹⁴ *J. hindsii* has recently been considered a variant of *J. californica* by Manning (1957), but the status of these two species is still in doubt (Manning, *in litt.*).

characteristic wing pattern (Fig. 195) which distinguishes it from other known species of *Rhagoletis*. The basal crossband is lacking or present only as a faint brownish yellow shading in the region of the humeral crossvein and over cell m.

Description. Body and wing measurements in Tables 10A–10B. Smallest representative of *suavis* group; no sexual dimorphism in body markings except for abdominal pollinose cream colored band along posterior margin of tergites II–IV in male and II–V in female. *Head* (Fig. 31): frontalia and parafrofrontalia light yellowish orange, ocellar plate brownish black, gularmentum and postgenae light cream, latter grading to dark yellowish orange dorsally; mentum golden tan; all other regions yellowish cream. Occipital, postorbital (6–13), postvertical (0–1), intravertical (0–1), genal, and well developed gular bristles dark yellowish orange; all other bristles black. *Thorax*: dorsum golden tan evenly covered with decumbent light yellow setae and whitish yellow microtrichia not arranged in vertical bands. Dorsocentrals slightly behind anterior supraalar; two pairs cream to light yellow scapulars. All pleural and sternopleural regions yellowish orange except for slightly lighter cream colored notopleural stripe. Two mesopleural bristles of about equal size. Halteres lemon yellow. Scutellum whitish with slight tint of yellow near base; postscutellum yellowish orange. A black spot above base of wing. *Legs*: all segments yellowish cream. Setae and bristles dark yellowish orange except variable black to yellowish cream postventral row of bristles on femur I; spurs on tibia II black; a single row of straight, short, dark yellowish orange setae on anterior-outer surface of tibia III, the latter also with short spur on anterior apex. *Wing* (Fig. 195): pattern distinctive in having no basal crossband. Apical band usually not joined to subapical band on costal margin; fuscated areas present along veins R_{4+5} and M_{1-2} between subapical and apical bands, these areas normally not

joined to either crossband. Junction of R_{2+3} and R_{4+5} with up to two setae on dorsal surface, one seta on ventral surface; R_{4+5} with up to five setae on dorsal surface. Crossvein r-m slightly closer to m than M_3 . Anal cell strongly pointed. *Abdomen*: all segments light cream without black markings. Some specimens with gray to brown appearance caused by internal decomposition. A faint lighter cream colored band present along posterior margin of tergites II–IV in male and II–IV or V in female. *Genitalia: male*—epandrium and surstyli (Figs. 72, 99) cream to light yellow; aedeagus (Fig. 130) resembling *suavis* (Fig. 129) with a finger-like apical appendage covered with short setae at tip; genital ring pouch well developed; phallic apodeme straight, surstyli straight, not bent at prensisetae. Ejaculatory apodeme normal (Fig. 142). *Female*—variation in ovipositor length in Fig. 20; ovipositor sheath golden yellow; three slightly club-shaped spermathecae with minute appressed scale-like papillae (Fig. 160); ovipositor with two pairs preapical setae.

Geographical variation. All specimens studied were from either Arizona or New Mexico, with the exception of one male from northern Utah and a female from southern Durango, Mexico. No geographical variation in body size was noted other than the normal wide variation common in this group.

Chromosome number and morphology (Fig. 221). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *J. major*, Indian Creek Campground, 6 mi. S. of Prescott, Arizona, 6,000 ft., 27 Aug. 1961; Southwest Research Station, Chiricahua Mts., Cochise Co., Arizona, 30 Aug. 1961; Nombre de Dios, Durango, Mexico, 6500 feet., 6 Sept. 1961.

Parasites. An *Opius* species near *ferrugineus* Gahan (Hymenoptera, Braconidae) and a *Eucolia* species (Hymenoptera, Cynipidae) have been collected in Arizona from walnuts heavily infested with *juglandis* (Flanders, 1961, personal communication). Both of these genera have species which parasitize *Rhagoletis*; therefore, it is likely that the two species mentioned are associated with *juglandis*.

Hosts. This species has been reared from *Juglans regia* L. variety in Arizona (Cresson, 1920; Brooks, 1921; Boyce, 1934; and others). *J. major* (Torr.) Heller (= *rupestris* of authors) has also been recorded as a host by Boyce (1934), and I have been able to rear *juglandis* from the fruits of this host collected in Arizona and Nombre de Dios, Durango, Mexico.

R. juglandis is sympatric with *boycei* over part of its range in Arizona and both of these species utilize the same species of *Juglans*.¹⁵ A discussion of the relationships between the two species and their hosts will be found in the host section of *boycei*.

Distribution (Map 7). *R. juglandis* normally reaches its northernmost limits in Arizona and southwestern New Mexico. Its range extends southward along the Sierra Madre Occidental as far south as at least southern Durango and possibly farther whenever suitable hosts are available. The single record from Utah probably represents a recent extension of the northern limits of *juglandis* as walnuts are not native to this area and have only recently been introduced for commercial and ornamental purposes.

Rhagoletis boycei Cresson

Rhagoletis boycei Cresson, 1929, Trans. Amer. Ent. Soc., 55: 413, pl. 16, fig. 10. [Holotype examined: ♂, Carr Canyon, Huachuca Mts., Cochise Co., Arizona, 13 August 1929, Persian walnut (A. M. Boyce) (ANSP, No. 6342); paratypes examined: 1 ♂ 1 ♀, same data as holotype.] —Boyce, 1934, Hilgardia, 8: 377–378, figs. 4D, 13, 15 (redescription, notes on biology).

Diagnosis. *R. boycei* is the only black species in the walnut infesting group. It can also be easily distinguished from all other *Rhagoletis* by the typical wing pattern (Fig. 194) which bears some resemblance to its closest relative, *zoqui* (Fig. 196), and to *juglandis* (Fig. 195). The presence of black vertical bands on the postgenae and lateral margins of the postcranium are also features found in no other members of the *suavis* group. The anal cell is not as pointed in this species, nor is the genital ring pouch as conspicuous as in other members of the species group.

Description. Body and wing measurements in Tables 10A–10B. *Head* (Fig. 27): upper medial part of postcranium light yellow grading to tan ventrally; postgenae and lateral margins of postcranium black, anterior margins of postgenae yellowish cream grading to white dorsally. Postorbital regions cream; lower half of frontalia dark yellowish orange grading to lighter yellow dorsally; parafrontalia cream; face, parafacialia, and genae dark yellowish orange; gulamentum light yellow; ocellar plate and mentum black. Postvertical, occipital, genal, and weakly differentiated gular bristles light yellow; all other major bristles, including 7–13 postorbitals, black. *Thorax*: all regions black except for cream colored notopleural stripe, halteres, and scutellum, the latter tinged with black near base; postscutellum shining black. Dorsum covered with cream colored to light yellow setae and microtrichia, without vertical banded pattern; dorsocentrals slightly behind anterior supraalars; two pairs deep cream to cream colored scapular bristles; two mesopleural bristles of about equal size. *Legs*: coxae black, trochanters light yellow, femora and bristles black, except knees which grade to golden yellow. Semierect setae on anterior surface of femur II absent, though present in other members of this species group. Tibiae I and II light yellow with black shading; tibia III black grading to yellow at apices; about 6 to 10 strongly developed semierect black setae on

¹⁵ See Manning (1957) for recent revision of *Juglans* in Mexico and southwestern United States.

anterior surface. All tarsal segments light yellow. *Wing* (Fig. 194): similar to *juglandis* and *zoqui* in having fuscated areas on veins R_{4+5} and M_{1+2} between apical and subapical bands. Medial band not reaching posterior margin of wing as in *zoqui*. Usually one seta ventrally and two setae dorsally at junction of veins R_{2+3} and R_{4+5} , occasionally both absent; R_{4+5} with 4–5 setae on dorsal surface. Anal cell bluntly pointed, not as well developed as in other members of this species group. Crossvein r-m closer to m than M_3 . *Abdomen*: all segments black in both male and female with tergites II–IV in male (Fig. 65) and II–V in female (Fig. 66) with white band on posterior margin; tergite V of male sometimes with yellowish orange area at apex. Both sexes sometimes with two narrow white spots on either side of medial line along posterior margin of tergite I. *Genitalia: male*—epandrium black, surstyli golden brown (Figs. 76, 95); aedeagus (Fig. 132) with rake-like appendage at tip resembling *completa* and *zoqui*; genital ring pouch small, not as strongly developed as in other members of *suavis* complex; phallic apodeme straight. Ejaculatory apodeme normal (Fig. 144). *Female*—variation in ovipositor length shown in Figure 20; ovipositor sheath shining black. Three cylindrical spermathecae with minute appressed scale-like papillae (Fig. 161) similar to those of *suavis* and *completa*; ovipositor with two pairs of minute preapical setae.

Geographical variation. The specimens examined were all from Arizona and other than a wide range in the size of individuals from the same locality no trends were found between individuals from different areas within the state.

Chromosome number and morphology (Fig. 222). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetid and a single pair of acrokinetic dot chromosomes. No morphologically distinguishable heterochromosomes or secondary constrictions were noted.

Source of cytological material: *Juglans major*, Onion Saddle Pass, Cochise Co., Arizona, 7500 ft., 30 Aug. 1961.

Courtship behavior. The courtship behavior of this species was not studied. Males were found patrolling ripe walnuts as do *suavis* and *completa* and are probably territorial.

Hosts. *R. boycei* has been reared from *Juglans major* (Torr.) Heller (= *rupestris* of authors, see Manning, 1957) and *J. regia* L. variety (Cresson, 1929; Boyce, 1934).

Distribution (Map 7). *R. boycei* apparently has a spotty distribution in Arizona and is more difficult to locate than the sympatric walnut infesting species, *juglandis*. I was able to locate a heavy infestation of *boycei* only at Onion Saddle Pass, Arizona, where *juglandis* appears to be abundant below 5,000–6,000 ft., and *boycei* above this altitude. The extent of overlap and emergence peaks were not determined. *R. boycei* has been collected in Arizona at altitudes up to 9,000 ft., and probably infests the native Arizona black walnut at its maximum altitude. Boyce (1934) was able to collect *juglandis* and *boycei* from the same grove, but I was unable to locate sympatric populations. This species apparently is restricted to southwestern New Mexico and Arizona and northern Sonora, Mexico.

*Rhagoletis zoqui*¹⁶ new species

Types. Holotype ♂, Zacualtipan, Hidalgo, Mexico, 15 Sept. 1961 (G. L. Bush) (MCZ, No. 30827); paratypes: 10 ♂♂ 10 ♀♀, Zoquizoquipan, Hidalgo, Mexico, 29 Oct. 1960 (USDA Mex. Fruit Fly Lab.) (MCZ).

Diagnosis. Differs from *boycei*, its nearest relative, in being much larger (Tables 10A–10B) and in having the black areas of the body reduced to only the pleural and sternopleural areas of the thorax in the male. The rest of the body ranges from

¹⁶ This name represents a noun in apposition with the abbreviation of Zoquizoquipan, the place where the species was first collected.

tan to yellow. In the female, the black markings are limited to isolated spotting on the pleural regions. The dorsum in both sexes is golden tan. The wing pattern is similar to that of *boycei* (Figs. 194, 196) but is more extensively marked along veins R_{4+5} and M_{1+2} between the apical and subapical bands and bears a third horizontal marking in cell R_5 between the fuscous markings along R_{4+5} and M_{1+2} . All three horizontal bands may or may not be joined to the apical and subapical crossbands.

Description. Body and wing measurements in Tables 10A-10B. *Head* (Fig. 29): posternum and frons yellowish orange; face slightly deeper yellow; mentum and postgenae tan, latter grading to yellowish orange dorsally. Postvertical, postorbital (5-12), and genal bristles black; occipital and well developed gular bristles yellowish orange; all other bristles black. *Thorax: male*—dorsum golden tan, covered by yellowish orange to yellowish tan setae and microtrichia not forming pattern of vertical stripes; dorsocentrals slightly behind anterior supraalars; two pairs yellowish orange scapular bristles with outer pair occasionally black, medial pair sometimes doubled. Two mesopleural bristles of about equal length. Pleural and sternopleural regions predominantly black. Notopleural stripe and scutellum light yellow, the latter grading to yellowish orange at base; postscutellum with two broad reddish brown vertical bands; halteres yellowish orange. *Female*—dorsum, scutellum, postscutellum, notopleural stripe, and halteres as in male. Pleural region not as heavily marked with black, predominantly yellowish tan; black markings usually limited to small isolated patches. The intensity of markings in some heavily marked females approaching coloration of some lightly pigmented males. *Legs: male*—coxae I and II dark shining brown; coxa III yellowish orange with brown markings on posterior surface. Trochanters yellowish orange. All bristles black. Femora black grading to yellowish orange at extremities; femur II with row of

semierect short bristles on anterior surface. Tibiae I and II tan grading to dark tan or black at base. Tibia III black with extremities grading to yellowish orange, with row of approximately 15 well developed semierect bristles along anterior outer margins. *Female*—all segments yellow to yellowish orange with black bristles, in striking contrast to those of male. *Wing* (Fig. 196): similar to pattern of *boycei* but with fuscous markings along R_{4+5} and M_{1+2} sometimes joined to crossbands. A third transverse band present in cell R_5 parallel to fuscous marking on R_{4+5} and M_{1+2} . Junction of apical and subapical crossbands on costa in cell R_1 constricted, much narrower than normal width of either crossband, occasionally completely separated by hyaline area as in *juglandis*. Up to three setae dorsally and usually two setae ventrally at junction of R_{2+3} and R_{4+5} ; four to eight setae on dorsal surface of R_{4+5} . Anal cell strongly pointed, with r-m closer to crossvein m than to M_3 . *Abdomen: male* (Fig. 61)—tergites II-IV with white band along posterior margin; tergites I-II yellowish orange, tergite III yellowish orange with two broad brownish black ovoid spots on either side of medial line; tergite IV mostly black, usually with some yellowish orange on medial line and outer margins; tergite V entirely brownish black. *Female* (Fig. 62)—tergites yellowish orange without brownish black markings; tergites II-V with white band along posterior margin. *Genitalia: male*—epandrium brownish black, surstyli dark yellowish orange (Figs. 78, 98); genital ring pouch well developed; phallic apodeme straight; aedeagus with rake-like apical appendage (Fig. 133); vesica bifurcate. Ejaculatory apodeme normal (Fig. 143). *Female*—variation in ovipositor length shown in Figure 20; ovipositor sheath dark brown. Three cylindrical spermathecae, tips somewhat pointed (Fig. 159), one usually about half as long as other two. Two pairs minute preapical setae on ovipositor tip.

Chromosome number and morphology

(Fig. 223). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *Juglans mollis*, Zoquizoquipan, Hidalgo, Mexico, Oct. 1957, and Sept. 15, 1961.

Courtship behavior. Males were found patrolling on walnuts, indicating that this species is territorial. No courtship behavior was observed.

Parasites. No parasites were reared from the material collected on two separate occasions at Zoquizoquipan, Mexico.

Hosts. This species has been reared only from *Juglans mollis* Engelm. (Nogal, Nogal encarcelada, nuez meca). Manning (1957) lists the known distribution for this species of walnut as Nuevo Leon, Tamaulipas, San Luis Potosi, Guanajuato, and Puebla, Mexico. It is apparently not sympatric with any other species of *Juglans* in Mexico. An infestation of larvae resembling *zoqui* was also found near Cuernavaca, Mexico, July 31, 1962, on what is probably *J. major* var. *glabrata* (Manning, 1963, *in litt.*).

Distribution (Map 7). Known only from the type locality and the nearby settlement Zoquizoquipan, Hidalgo, Mexico.

TABELLARIA SPECIES GROUP

Benjamin (1934) was the first to suggest that Cresson's 1929 revision of the genus *Rhagoletis* lumped too extensively. This is particularly true in the case of the *tabellaria* group where Cresson recognized only one species, *tabellaria*, and regarded *juniperina* and *ribicola* as mere "varieties" that did not merit recognition under a separate name. Careful examination reveals that Cresson's "varieties" are actually quite distinct and include representatives from two species groups. These groups seem to be either convergent for several characters such as wing pattern and body coloration,

or have retained these features through parallel evolution.

The *tabellaria* group consists of four species: *tabellaria*, *juniperina*, *persimilis*, and *ebbettsi*. This is probably a conservative number; *tabellaria* itself may prove to represent two sibling species when more is known about its biology (see host section of *tabellaria*). *R. ribicola*, regarded by Cresson as a synonym of *tabellaria*, is now placed in a group of its own in which *berberis* tentatively has been included. There is good morphological evidence that both groups probably originated in the Old World and may include several Eurasian species, but the affinities are as yet unclear.

Diagnosis. The *tabellaria* group is distinguished from the *ribicola* group on the basis of genitalic characters. In the *tabellaria* group the spermathecae are globular and attached to the spermathecal ducts by a well sclerotized cylindrical tube (Figs. 162–165). This is in contrast to the long cylindrical spermathecae of the *ribicola* group (Figs. 166–167). There are always three spermathecal ducts, but the number of spermathecae may vary from two to three. The aedeagus is also distinctive (Figs. 123–125). The vesica is somewhat convoluted in the *tabellaria* group and there is, at most, only a very small finger-like apical appendage which is never setulose. In *ribicola* and *berberis* the aedeagus has a relatively large finger-like apical appendage which is covered by well developed straight setae; the vesica is smooth (Figs. 126–127).

The *tabellaria* group can be distinguished from all other *Rhagoletis* groups by its wing pattern, genitalia, and body coloration.

Rhagoletis tabellaria (Fitch)

Tephritis tabellaria Fitch, 1855, Trans. New York State Agr. Soc., 1854, 14: 770. [Type lost.]¹⁷ —Fitch, 1856, 1st and 3rd Rept., Noxious and Beneficial Insects of New York: 66 (reprint of 1855 paper).

¹⁷ A neotype was not designated pending a more complete study of both the eastern and western populations of this species.

	<u>R. tabellaria</u> East. pop.	<u>R. tabellaria</u> West. pop.	<u>R. juniperina</u>	<u>R. persimilis</u>
n	14	14	3	5
HL	.79±.026 (.51-.89)	.70±.022 (.56-.86)	.78 (.68-.90)	.96 (.92-1.00)
HW	1.24±.040 (.77-1.38)	1.11±.031 (.88-1.23)	1.33 (1.08-1.57)	1.42 (1.38-1.50)
HH	1.09±.034 (.66-1.17)	.91±.027 (.73-1.05)	1.10 (.87-1.28)	1.23 (1.16-1.28)
LW	.57±.019 (.35-.66)	.51±.014 (.42-.58)	.72 (.53-.80)	.63 (.62-.65)
EH	.82±.028 (.52-.99)	.73±.021 (.62-.83)	.88 (.70-1.04)	.99 (.97-1.03)
FrWV	.48±.017 (.30-.57)	.43±.013 (.34-.53)	.44 (.34-.66)	.57 (.56-.60)
AL	.42±.013 (.28-.47)	.39±.011 (.33-.45)	.41 (.36-.45)	.47 (.45-.50)
FL	.58±.019 (.40-.65)	.49±.016 (.40-.60)	.61 (.51-.71)	.66 (.62-.69)
GW	.17±.009 (.10-.20)	.16±.007 (.11-.21)	.20 (.15-.25)	.19 (.17-.21)
TL	1.57±.056 (.95-1.82)	1.35±.046 (1.06-1.64)	1.79 (1.23-1.85)	1.98 (1.88-2.09)
n	11	14	10	5
WL	3.18±.053 (2.91-3.40)	2.85±.077 (2.37-3.37)	2.45±.070 (2.11-2.79)	3.46 (3.42-3.52)
WW	1.70±.036 (1.50-1.90)	1.53±.048 (1.21-1.80)	1.27±.028 (1.16-1.44)	1.72 (1.64-1.80)

Table 11A. Body and wing measurements of males of the tabellaria species group. Figures represent mean, standard error, and range.

	<u>R. tabellaria</u> East. pop.	<u>R. tabellaria</u> West. pop.	<u>R. juniperina</u>	<u>R. persimilis</u>
n	6	12	16	7
HL	.77 (.65-.87)	.73±.016 (.64-.79)	.82±.025 (.61-.96)	1.01 (.93-1.07)
HW	1.27 (1.16-1.38)	1.19±.021 (1.05-1.28)	1.37±.043 (1.10-1.68)	1.53 (1.47-1.55)
HH	1.02 (.83-1.12)	.97±.029 (.73-1.05)	1.11±.036 (.91-1.35)	1.29 (1.24-1.36)
LW	.59 (.51-.62)	.55±.012 (.46-.63)	.68±.021 (.53-.83)	.68 (.65-.70)
EH	.83 (.70-1.93)	.79±.020 (.67-.87)	.91±.027 (.73-1.10)	1.05 (1.03-1.08)
FrWV	.48 (.37-.56)	.45±.013 (.38-.51)	.54±.024 (.40-.71)	.60 (.56-.64)
AL	.43 (.36-.50)	.40±.008 (.35-.43)	.43±.009 (.37-.49)	.50 (.48-.51)
FL	.56 (.45-.62)	.53±.013 (.46-.60)	.66±.022 (.50-.80)	.79 (.75-.83)
GW	.16 (.12-.20)	.15±.006 (.12-.19)	.21±.009 (.16-.25)	.21 (.19-.25)
TL	1.66 (1.44-1.81)	1.48±.037 (1.28-1.69)	1.70±.061 (1.33-2.08)	2.11 (2.03-2.20)
n	6	12	11	7
WL	3.36 (3.07-3.70)	3.19±.068 (2.70-3.70)	2.84±.065 (2.59-3.42)	3.80 (3.46-3.96)
WW	1.84 (1.64-2.06)	1.75±.052 (1.41-2.13)	1.50±.048 (1.24-1.79)	2.03 (1.76-2.14)

Table 11B. Body and wing measurements of females of the tabellaria species group. Figures represent mean, standard error, and range.

(*Trypeta*) *tabellaria*, —Loew, 1862, Smithson. Misc. Coll., 6: 60.

Trypeta (*Rhagoletis*) *tabellaria*, —Loew, 1873, Smithson. Misc. Coll., 11: 263–265, 329, 338–339 (redescription).

Rhagoletis tabellaria, —Doane, 1898, Ent. News, 9: 69 (in key). —Aldrich, 1909, Canad. Ent., 41: 69 (in key). —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 18 (in key, distribution). —Phillips, 1923, J. New York Ent. Soc., 31: 122, 134 (in key, wing figured). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 406–407 (redescription, in key, wing figured). —Curran, 1932, Amer. Mus. Nov., 526: 3, 5 (in key, wing figured). —Pickett, 1937, Canad. J. Res. (D), 15: 62 (genitalia).

Diagnosis. *R. tabellaria* is distinguished from all other North American *Rhagoletis* species by the following characters: (1) the apical end of the phallotheca bears a tubular sac (Fig. 123, S); (2) there are three spermathecal ducts but only two globular spermathecae (Fig. 162); (3) the basal and medial wing bands are diffusely coalesced over a broad area along the posterior margin of the wing (Fig. 197); (4) the femora are predominantly black; (5) there is a horseshoe-shaped black marking on the posterior surface of the head. The only species with which *tabellaria* can be confused is *persimilis*, which has three conical, pine-cone shaped spermathecae (Fig. 165) and lacks the tubular sac on the apex of the phallotheca.

Description. Body and wing measurements in Tables 11A–11B. **Head** (Fig. 34): postcranial and posterior two-thirds of postgenal regions forming a brownish black horseshoe shaped pattern; mentum and ocellar plate brownish black; antennae and lower half of frons yellowish orange, parafacials slightly lighter (light yellow to white); face and parafacialia white, densely covered with microtrichia; genae, anterior margin of postgenae, and postorbital regions white, occasionally faintly tinted with yellow. Occipital and hair-like gular bristles light yellow, all other bristles black, including weak genal bristle; 5–12 postorbitals; postverticals short, often lacking; single intravertical usually present. **Thorax** (Fig. 46): dorsum brownish black to black

with four well defined parallel vertical stripes; outer pair broken by transverse sulcus, posterior section reaching line drawn between posterior supraalars; medial pair reaching from scapulars to base of pre-scutellars. Dorsocentrals in line with anterior supraalars; two pairs black scapular bristles, each pair occasionally with extra smaller bristles arranged in tandem; usually one mesopleural bristle; a second, much smaller, lower bristle occasionally present, variable in size. Notopleural stripe and circular scutellar spot white, latter extending from apex to a line drawn between basal scutellars; postscutellum shining black; halteres light tan to yellow. **Legs:** coxae and femora mostly black, femur I with some yellowish orange on anterior apical surface. Trochanters, tarsi, and all tibiae almost entirely light yellow; tibiae II and III with black shading near base; single row of stout semierect black setae on outer anterior surface of tibia III. **Wing** (Fig. 197): pattern consisting of two V's, one of which is inverted; basal and medial bands coalesce over broad area between anal cell and posterior margin of wing; apical and subapical bands joined on costa; hyaline region between apical band and costa. Junction of R_{2+3} and R_{4+5} bare; R_{4+5} bare over entire length. Anal cell sharply pointed (Fig. 180). **Abdomen** (Figs. 57–58): all segments brownish black to black with posterior margin of tergites II–IV in male, II–V in female with white to grayish white band. **Genitalia: male**—epandrium black, surstyli dark yellowish orange, of uniform width over most of length, tapering abruptly to blunt point near apex (Figs. 85, 101); end of phallotheca at junction with aedeagus with gland-like tubular sac (Fig. 123, S); vesica convoluted; aedeagal tip bearing small, narrow, finger-like appendage, most easily observed with phase contrast optics; ejaculatory apodeme normal (Fig. 146). **Female**—variation in ovipositor length shown in Figure 17; ovipositor with two pairs minute preapical setae; ovipositor sheath black; three sper-

mathecal ducts and two globular spermathecae with thickened bases; spermathecae covered with long scale-like papillae (Fig. 162).

Geographical variation. No differences in either size (see Tables 11A–11B) or color pattern were noted between the eastern and western populations of this species.

Chromosome number and morphology (Fig. 226). The diploid number in both sexes is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No secondary constrictions or morphologically differentiated heterochromosomes (XY) were observed.

Source of cytological material: *Cornus amomum*, Blue Hills, vicinity Milton, Mass., 4 July 1963; *Vaccinium* spp., vicinity Montezano, Wash., 16 July 1961.

Hosts. The eastern population of *tabellaria* has been found associated only with the genus *Cornus* (Cornaceae). Glasgow (1933) reported infestations in *C. stolonifera* Michx., and I have been able to rear it from *C. amomum* Mill. growing in the vicinity of Boston, Mass. *C. amomum* is also infested by *R. cornivora* (Hall, 1943), a member of the *pomonella* group, but I have not found the two *Rhagoletis* species infesting berries on the same plant. However, there is a single specimen of *tabellaria* in a series from the CNC which Hall reared from *C. amomum* during his studies on *cornivora* in Canada (Hall, 1938, 1943). This would indicate that mixed populations of these two species may possibly occur.

The western representatives of *tabellaria* apparently infest only the fruits of *Vaccinium* (Ericaceae) (Plank, 1923; Phillips, 1946) (for details of distribution see Camp, 1942). *Cornus* is not known to be attacked by *tabellaria* west of the 98th meridian, although the same species serving as hosts in the East occur all the way to the west coast. Ecological factors other than host specificity must restrict eastern *tabellaria*

to the more mesophytic regions of north-eastern North America.

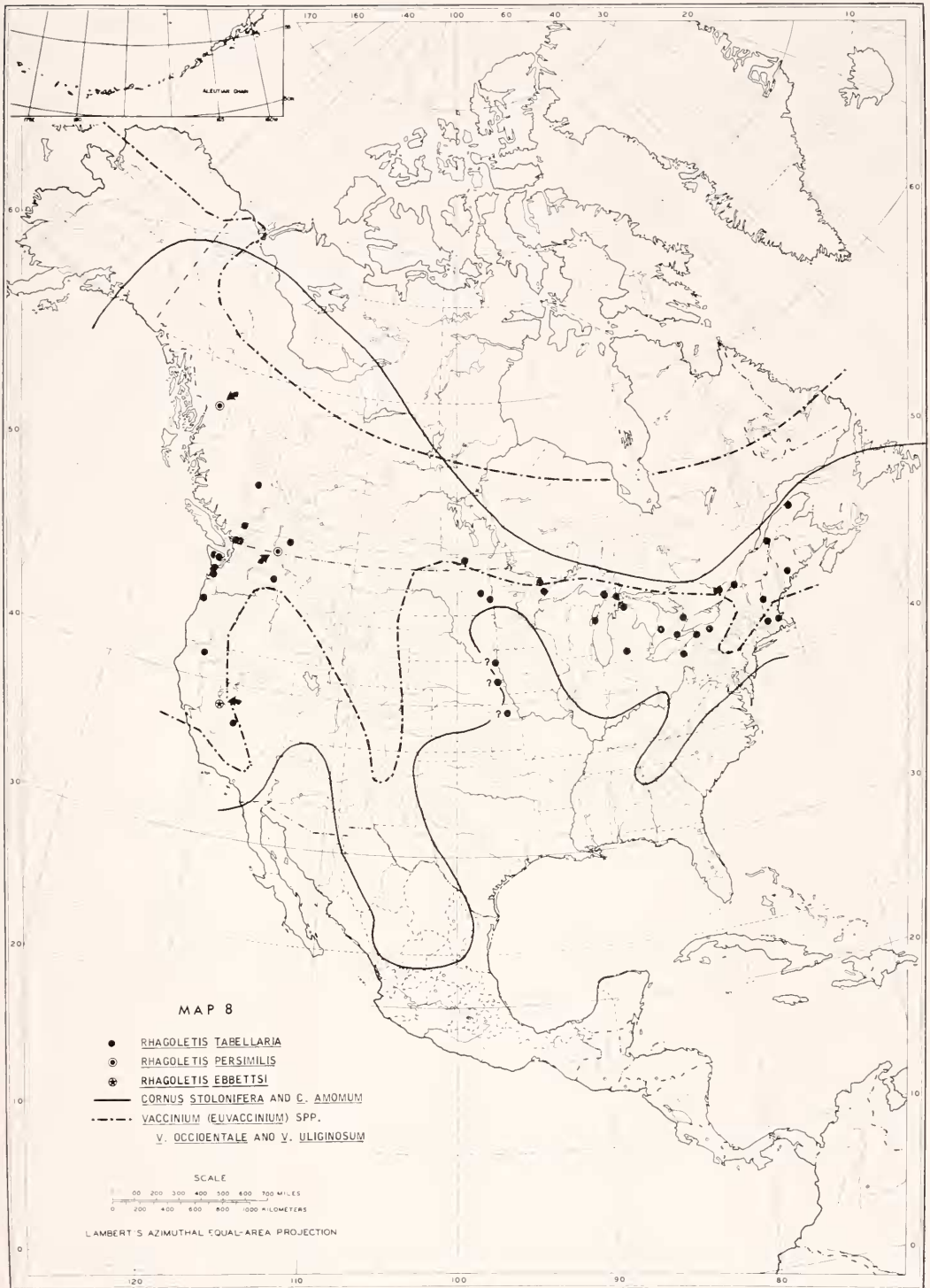
The eastern population is also apparently unable to infest *Vaccinium*, or is excluded from this host by the presence of *mendax* (*pomonella* group). *R. mendax*, however, does not occur over the entire range of eastern *tabellaria*, and *tabellaria* seems to have no trouble holding its own against the other sympatric competing *Cornus* infesting species, *cornivora* (*pomonella* group). Competitive exclusion, therefore, does not seem to be the explanation for the difference in host preference between the two allopatric *tabellaria* populations.

These two allopatric populations probably represent distinct species even though morphological differences were not detected. Sibling species pairs showing similar amphicontinental distributional patterns are found in other *Rhagoletis* groups, such as *pomonella*–*zephyria* and *cingulata*–*indifferens*, which infest either closely related or different hosts.

Further details regarding the distribution and history of *Cornus* and *Vaccinium* may be found in the host sections of *cornivora* and *mendax*.

Distribution (Map 8). *R. tabellaria* is represented by two distinct allopatric and allotrophic populations. The northernmost limits of the eastern race appear to coincide with the northern limits of its host, *Cornus*. As with many eastern species of *Rhagoletis*, its western limits do not extend beyond the 100th meridian. Its southern limits are less well known, and it may occur farther south than indicated on the map. The three localities accompanied by question marks represent single individuals which are somewhat morphologically distinct from both the eastern and western populations and may represent a third distinct species. In the absence of suitable material or accompanying host data, I have included them with *tabellaria*.

The distribution of the western race is



more spotty and probably extends farther north and east.

Rhagoletis juniperina Marcovitch

- Rhagoletis juniperinus* Marcovitch, 1915, Ann. Ent. Soc. Amer., 8: 171-173, pl. 13, figs. 4-7. [Lectotype ♂, by present designation, Six Mile Creek, Ithaca, N.Y. (MCZ, No. 7723; cotype, CU, No. 510.2).] —Phillips, 1923, J. New York Ent. Soc., 31: 134, 135, pl. 18, fig. 19 (in key, host). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 26, 69-70, figs. 26, 71, 129, 130, 173 (larval morphology, in key). —Hering, 1958, Stuttgarter Beitr. z. Naturkunde, 7: 4 (comparison with *R. flavigenualis*).
Rhagoletis tabellaria, —Cresson, 1929 (in part), Trans. Amer. Ent. Soc., 55: 406-407 (variety of *tabellaria*).
Rhagoletis juniperina, —Rohdendorf, 1961, Ent. Obozr., 40: 176 (justified emendation of incorrect original spelling).

Diagnosis. The following combination of characters distinguish *juniperina* from other members of the *tabellaria* and *ribicola* groups: (1) basal and medial wing bands are not joined along the posterior margin of the wing; (2) there is no black shading on the posterior lower lateral half of the head; (3) all femora are black; (4) the surstyli are straight, short and sharply pointed (Fig. 83); (5) the spermathecae are globular and covered by many small sharply pointed scale-like papillae (Fig. 163).

Description. Body and wing measurements in Tables 11A-11B. **Head** (Fig. 36): black stripe across lower two-thirds of posteranium but not extending ventrally over postgenae. Postorbitals, upper one-third of posteranium, and lower half of frons light yellowish orange; parafrontalia, face including parafacialia, genae, and gumentum bright yellow; postgenae light yellow grading to slightly darker dorsally; mentum black. Occipital and genal bristles light yellow, all other major head bristles black; postverticals short, about as long as postorbitals (8-12); gular bristle not differentiated from other yellow setae on gumentum and postgenal regions. **Thorax** (Fig. 44): all regions concolorous black except for white notopleural stripe and

scutellar spot. Dorsum covered evenly with white to light yellow setae and microtrichia arranged in four faintly differentiated vertical rows, medial pair sometimes fused into single broad band; dorsocentrals slightly before a line drawn between anterior supralars; two pairs yellowish orange scapular bristles; two mesopleural bristles. Circular scutellar spot small, extending from apex between bases of apical scutellars cephalad to a point about one-half to two-thirds distance between apical and basal scutellar bristles. Postscutellum shining black; halteres light yellowish orange. **Legs:** variable in color, depending on locality. Coxae and femora black, latter ranging to yellow at knees to almost entirely yellow in some specimens from Manitoba. Trochanters brownish yellow; tibiae yellowish tan; tibia II with weak row of setae on outer posterior surface; tibia III bearing short row of semierect setae on outer anterior surface. **Wing** (Fig. 198): medial band not joined to either basal or subapical bands; hyaline area between apical band and costa. R_{4+5} bare; 0-3 setae at junction of R_{2+3} and R_{4+5} (0 in most eastern specimens, 1-3 in specimens from California). Crossvein r-m equidistant from m and M_3 . Anal cell pointed (Fig. 178). **Abdomen:** as in *tabellaria* (see Figs. 57, 58); base color dark brown to brownish black, posterior margin of tergites II-IV in male, and II-V in female with whitish pollinose band. **Genitalia:** male—epandrium black, surstyli yellowish orange, straight and sharply pointed, slightly narrowed between prenisetae and base (Figs. 83, 103). Aedeagus without apical appendage (Fig. 125); vesica smooth; ejaculatory apodeme normal (Fig. 150). **Female**—variation in ovipositor length shown in Figure 17; ovipositor sheath black, ovipositor tip with three minute preapical setae. Three spermathecal ducts; two globular spermathecae, each with large, somewhat barrel-shaped cylindrical base and covered by long sharply pointed scale-like papillae (Fig. 163).

Geographical variation. The specimens examined from California and Manitoba are markedly larger than those from eastern and southwestern United States (for example, see variation in ovipositor length, Fig. 17). The Manitoba specimens have more extensive areas of yellow markings on the legs, while those from California have a much larger scutellar spot and are the only specimens with one to three setae at the junction of R_{2+3} and R_{4+5} . They also have two or three mesopleural bristles instead of the usual one.

Chromosome number and morphology (Fig. 227). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetin chromosomes and a single pair of acrokinetic dot chromosomes. A secondary constriction was noted in early metaphase plates on the short arms of one chromosome pair. No heteromorphic sex chromosomes (XY) were observed.

Source of cytological material: *Juniperus virginiana*, Lincoln, Mass., Oct. 10, 1962.

Courtship behavior. The courtship behavior of this species has not been studied.

Hosts. *R. juniperina* and other species of Tephritidae which infest *Juniperus* (Cupressaceae) apparently restrict their attacks to species of Section *Sabina*. No tephritid, as far as is known, infests any species of Section *Oxycedrus*. *R. juniperina* has been reared from *Juniperus virginiana* L. at Ithaca, New York (Marcovitch, 1915; Phillips, 1946), and I have collected an adult and larvae from the same host in Lincoln, Mass. A single specimen of *juniperina* has also been reared from *J. monosperma* (Engelm.) Sarg. growing in Oak Creek Canyon, Arizona.

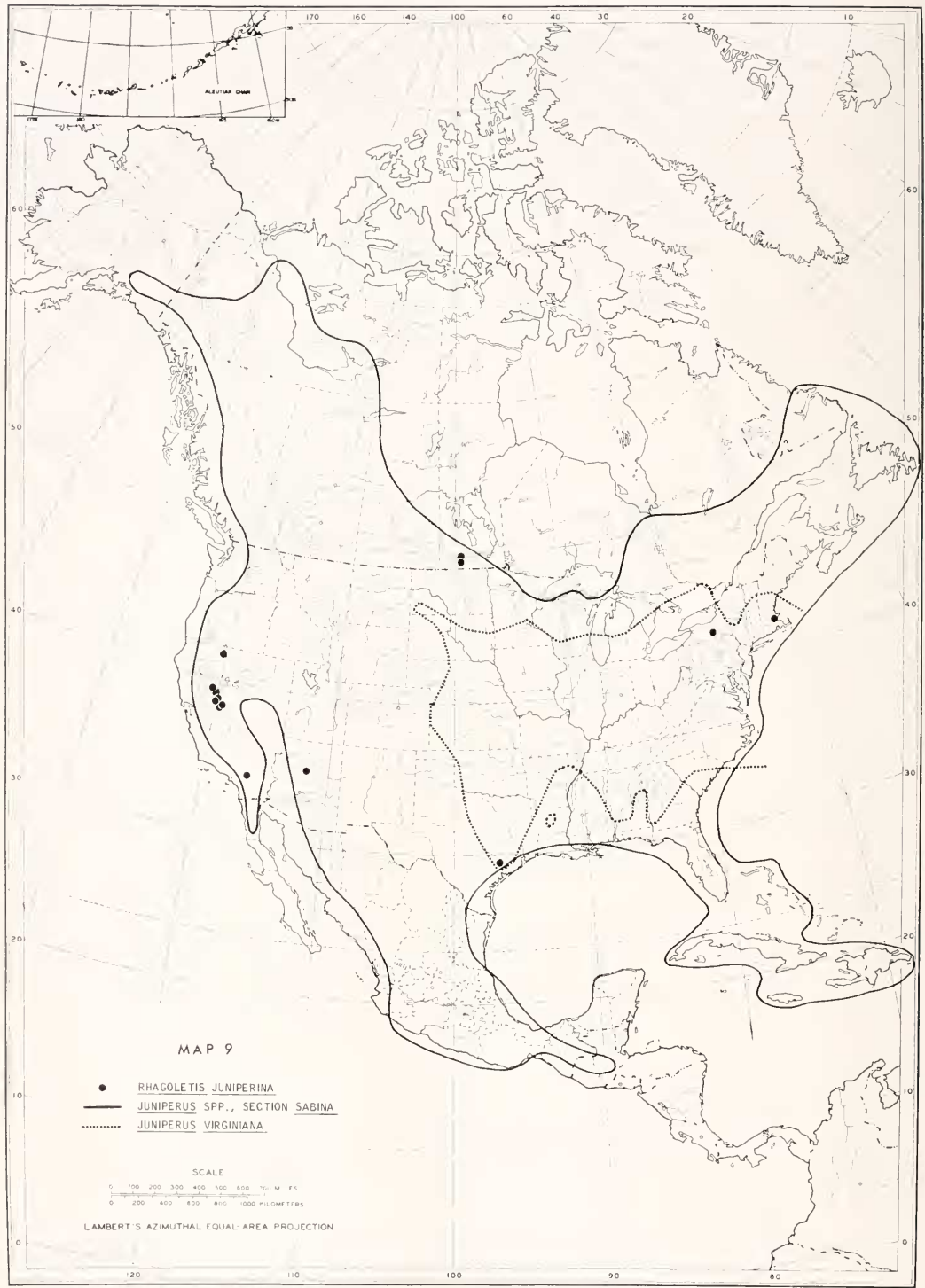
The presence of *juniperina* in Manitoba and California, beyond the range of its two recorded hosts, suggests that this fly infests other species of *Juniperus*, although no *Rhagoletis* have ever been recorded from juniper in the far western part of the United States. The host relationships of these western populations are therefore in doubt. The Manitoba and particularly the Cali-

fornia populations may represent new species. *Rhagoletis flavigenualis*, whose wing pattern bears some resemblance to that of *juniperina*, has been reared from *J. excelsa* Bieb. (= *J. sabina* L. var. *taurica* Pall.) in Turkey (Hering, 1958). The only other species of Tephritidae associated with juniper is *Paraterellia varipennis* (Coquillett), which has been reared from *Juniperus occidentalis* Hook in California (Foote, 1960).

Section *Sabina* is widespread over North America (Map 9), Eurasia, and North Africa (see Florin, 1963, for details). Some North American species in the Section are closely related to Old World forms. This is true of *J. virginiana*, *J. horizontalis* Moench., and *J. scopulorum* Sarg., which Stebbins (1950) considers to be only well marked subspecies of the Old World *J. sabina*.

The past history of *Juniperus*, its present distribution in North America, and the existence of conspecific or closely related species in Eurasia and North America indicate that the genus was probably part of the Holarctic Arcto-Tertiary geoflora. Insects associated with juniper would undoubtedly follow a similar distributional pattern. On morphological grounds the closest relatives of *juniperina* appear to be Eurasian. It may therefore have arrived in North America sometime before or during the Pleistocene. It is also possible that *juniperina* arose from some North American *tabellaria*-like species. However, the morphology of *juniperina* is sufficiently different to suggest that it has not diverged recently from any North American representatives of the *tabellaria* group. The answer to this problem will have to await a study of the east Asiatic *Juniperus* and its associated insect species.

Distribution (Map 9). **CANADA:** MANITOBA: Carberry; vicinity of Stockton; Aweme. **U.S.A.:** MASSACHUSETTS: Lexington, Middlesex Co. NEW YORK: Ithaca, Tompkins Co. TEXAS: Schulenburg, Fayette Co. ARIZONA: Oak Creek Canyon,



Coconino Co. CALIFORNIA: Lake City, Modoc Co.; Woodfords, Alpine Co.; Big Bear Lake, San Bernardino Co.; Glen Aulin to Waterwheel Falls, Yosemite National Park; Norden, Nevada Co.; vicinity of Leavitt Meadows and vicinity of Sonora Pass, Mono Co.; Silver Lake, Amador Co.; Cathedral Lake Tahoe.

Rhagoletis persimilis new species

Types. Holotype ♂, Robson, British Columbia, 15 June 1947 (H. R. Foxlee) (CNC, No. S456); paratypes: 5 ♂♂ 6 ♀♀, same data as type (CNC, MCZ).

Diagnosis. Similar to *tabellaria* in color pattern but larger (Tables 11A–11B) and differing in the following characters: (1) longer ovipositor (Fig. 17); (2) there are three globular to somewhat cone-shaped spermathecae covered by small appressed scale-like papillae (Fig. 165); (3) the proctiger of the male is more elongate and densely covered with long fine setae near the apex (Fig. 86) resembling the proctiger of *Carpomyia vesuviana* A. Costa (see Silvestri, 1916); (4) the surstyli are more pointed and thicker at the base (Fig. 86) than those of *tabellaria* (Fig. 85); (5) the aedeagus (Fig. 124) is swollen medially, bears a small tuft of setae on the dorsal margin of the vesica, and has no gland at the apex of the phallosome.

Description. Body and wing measurements in Tables 11A–11B. *Head* (Fig. 33): entire posterior surface black grading to dark brown to brownish yellow in region of gulamentum; postorbital region, genae, parafrontalia, and entire face white to whitish yellow; frons light yellow, antennae yellowish orange. Postocellars yellow, all other major bristles black; setae on postgenae and gulamentum white. Usually one postvertical, 8–13 postorbitals, usually three, occasionally four, pairs of lower frontal orbital bristles. *Thorax*: black except for white notopleural stripe and scutellar spot, latter with V-shaped anterior margin reaching basally beyond line drawn between basal scutellars; lateral margins passing well

outside base of apical scutellars and ending below apex; postscutellum shining black, almost completely devoid of microtrichia; halteres yellow. One to two mesopleural bristles; anterior dorsocentrals located about in line with anterior supraalars; dorsum of thorax as in *tabellaria* (Fig. 46) with four distinct rows of white microtrichia and covered with yellow decumbent setae; outer row broken by transverse sulcus. *Legs*: all coxae and femora black; all tibiae yellow; trochanters I and II yellow, III yellow with black on posterior surface; tibia III with row of weakly developed semierect setae on anterior outer margin; tarsal segments yellow. *Wing* (Fig. 199): basal and medial bands joined broadly from middle to cell Cu₁. Preapical band joined to apical band from costa to just beyond R₄₊₅; hyaline area between apical band and costa. R₄₊₅ and junction with R₂₊₃ bare. Crossvein r-m about equidistant from m and M₃. Anal cell moderately pointed (Fig. 179). *Abdomen*: base color black with tergite V polished. Tergites I–IV in both sexes with white pollinose band along posterior margin; very narrow white band along posterior margin of tergite V in some females. *Genitalia: male*—epandrium black, surstyli yellow; proctiger elongate, densely covered with setae at apex; surstyli broad at base, tapering to sharp point (Fig. 86); fultella with distinct shelf behind base of curved phallic apodeme; aedeagus (Fig. 124) swollen medially; vesica with narrow finger-like appendage and small tuft of setae on dorsal margin; ejaculatory apodeme normal (Fig. 148). *Female*—variation in ovipositor length (Fig. 17); ovipositor with two pairs of preapical setae; ovipositor sheath shining black; three globular spermathecae somewhat cone-shaped, covered with very small scale-like papillae fused to surface; base enlarged and cylindrical.

Host. The host of this species is not known.

Distribution (Map 8). **CANADA:** BRITISH COLUMBIA: Bear Lake and Robson.

Rhagoletis ebbettsi new species

Type. Holotype ♀, 4 mi. E. Ebbetts Pass, Alpine Co., California, summer 1961 (R. P. Allen) (USNM, No. 67378); wing slide No. 313, ♀ genitalia No. 327 (G. L. Bush).

R. ebbettsi is being described from a single damaged specimen. The legs are missing, and the antennae and mouthparts are recessed into the head making it difficult to study details of these structures. The specimen is discolored from material used in NH₃ sticky traps.

Certain aspects of the wing pattern, spermathecae, and black markings on the posterior region of the head relate this species closely to *tabellaria* and *juniperina*.

Diagnosis. The striking wing pattern of *ebbettsi* (Fig. 200) in combination with the distinct pattern of the dorsum (Fig. 43) and globular spermathecae (Fig. 164) separate this species from all other North American *Rhagoletis*. The medial wing band is joined by a broad fuscous region in cell R₅ between R₄₊₅ and M₁₊₂ just apicad of r-m. The only species with which *ebbettsi* could be confused is *R. zernyi*, known only from the type specimen collected at Albarracin, Aragon, Spain in 1924 (Hendel, 1927). It can be differentiated from this species by the position of the connection between the subapical and medial crossbands. The posterior hyaline region between the medial and subapical bands reaches to R₄₊₅, completely bisecting cell R₅ in *zernyi*. In *ebbettsi* the junction covers cell R₅.

Description. *Head:* base color yellow, darkened and greasy, probably the result of residue from sticky trap. Postorbital and upper occipital regions yellow, rest of posterior surface of head with horseshoe shaped black mark grading to slightly brownish black ventrally; mentum black. Postverticals and gular bristles yellow, all other major bristles black, including small genal bristle; postgenae and gulamentum covered with scattered yellow setae; three postverticals on each side of occiput; outer-

verticals, right innervertical, and lower left lower fronto-orbital missing. Six postorbitals on left and eight on right, some missing. *Thorax:* base color black, dorsum (Fig. 43) covered by light yellow decumbent setae and white pollinose microtrichia arranged in four rows, fused anteriorly; two inner rows shorter than outer pair. Notopleural stripe and scutellar spot cream, possibly tinted with yellow in normal specimens; scutellar spot reaching from below apex anteriorly to line drawn between basal scutellars; lateral margins passing through base of apical scutellars. Postscutellum shining black. Left haltere missing, right haltere tan. Two mesopleural bristles, upper missing. Dorsocentrals in line with anterior supraalars; left dorsocentral missing. *Legs:* all segments except black coxa and yellow right trochanter II missing. *Wing* (Fig. 200): basal band not joined to medial band; medial band joined to subapical band in cell R₅ between R₂₊₃ and R₄₊₅ apicad of r-m; hyaline area between apical band and costa. R₄₊₅ bare over entire length and at junction with R₂₊₃. Anal cell bluntly pointed. Crossvein r-m about midway between m and M₃. *Abdomen:* black; tergites II-V with broad white pollinose bands along posterior margins as in *tabellaria* (Fig. 58). *Genitalia:* ovipositor with two preapical setae; 0.87 mm long, 0.18 mm wide; ovipositor sheath black. Two spermathecae covered by small appressed scale-like papillae, each with bulbous base and small apical knob (Fig. 164). Three spermathecal ducts.

Distribution (Map 8). Known only from the type locality.

RIBICOLA SPECIES GROUP

The *ribicola* group includes two species, *ribicola* and *berberis*. *R. berberis*, tentatively placed in this group, may actually be more closely related to certain European species which are also known to infest the genus *Mahonia* (*Berberis* of authors). *R. ribicola* was considered to be so closely related to *tabellaria* that Cresson (1929)

synonymized *ribicola* with *tabellaria*. The similarities, however, are only superficial. The two species in the *ribicola* group, particularly *ribicola* itself, seem to be more closely related to the *cingulata* group in North America and to *flavicincta* Loew in Europe.

Diagnosis. The characters which distinguish the *ribicola* group from the *tabellaria* group are restricted to the genitalia. Both *ribicola* and *berberis* have long cylindrical spermathecae covered with scattered, rather long scale-like papillae (Figs. 166–167). In members of the *tabellaria* group these organs are globular in shape (e.g., Fig. 162). The aedeagus in both *ribicola* and *berberis* has an apical appendage covered with short spike-like setae (Figs. 126–127). Members of the *tabellaria* group have no setulose apical appendage.

Rhagoletis ribicola Doane

Rhagoletis ribicola Doane, 1898, Ent. News, 9: 69–72. [Lectotype ♀, by present designation, (Washington Expt. Station No. 66) (USNM cotype No. 42213; MCZ type No. 17085).] —Aldrich, 1909, Canad. Ent., 41: 69, 72, pl. 4 (1) (in key). —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 7, 14–16, 19 (in key, discussion). —Marcovitch, 1915, Ann. Ent. Soc. Amer., 8: 173 (compared with *juniperina*). —Curran, 1932, Amer. Mus. Nov., 526: 3, 6–8. —Pickett, 1937, Canad. J. Res. (D), 15: 62 (genitalia). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 72–74, figs. 29, 74, 135, 176 (larval morphology, in key).

Rhagoletis tabellaria, —Cresson, 1929 (in part), Trans. Amer. Ent. Soc., 55: 406–407, pl. 16, fig. 5.

Diagnosis. There is a conspicuous sexual dimorphism in leg coloration of *ribicola* which Doane (1898) did not recognize in his original description. All segments except the coxae are yellow in the male, while in the female the coxae, as well as femora II and III are brownish black with yellowish knees. Femur I is entirely yellow or with brownish black shading on the posterior surface. This character, in combination with the wing pattern (Fig. 201), distinctive surstyli (Fig. 84), and strongly keeled ejaculatory apodeme (Fig. 147),

differentiates *ribicola* from *berberis* and all other North American *Rhagoletis*.

Description. Body and wing measurements in Tables I2A–I2B. **Head** (Fig. 37): posterior region and mentum brownish black, with postorbital, upper occipital, and postgenal regions cream to white. Frons, face, and genae light yellow, antennae slightly yellowish orange. Postocellar and genal bristles yellow; all other major bristles, including 1–2 postverticals and 8–14 postorbitals, brownish black to black. Gular bristle not differentiated from light yellow setae on postgenae and gulamentum. **Thorax:** dark brownish black except for cream colored notopleural stripe and scutellar spot, latter reaching anteriorly beyond a line drawn between basal scutellars; lateral margins reaching well outside base of apical scutellars. Dorsum with distinct pattern of four white pollinose stripes similar to that of *berberis* and *tabellaria* (Fig. 46). Outer stripes reaching from scapulars to line between posterior pair of posterior supraalars, broken by transverse sulcus; inner pair shorter, ending just behind line between dorsocentrals; dorsocentrals slightly before line drawn between anterior supraalars; one mesopleural bristle. Postscutellum shining black; halteres yellow. **Legs:** male—coxae and spurs black, all other segments and bristles yellow, including row of semierect bristles on anterior surface of tibia III. **Female**—coxa I, trochanters, tibiae and tarsal segments yellow; coxae and femora II and III dark brown to brownish black, latter grading to yellow at apices; femur I usually entirely yellow, occasionally with brown shading on posterior surface. **Wing** (Fig. 201): medial band not reaching posterior margin and not joined to basal or subapical bands. Hyaline region between apical band and costa. R_{4+5} bare over entire length and at junction with R_{2+3} . Anal cell variable, not strongly pointed; crossvein Cu_2 sometimes only slightly bowed (Fig. 176). **Abdomen:** shining black with pollinose white band along posterior margin of tergites II–IV in

	<u>R. ribicola</u>	<u>R. berberis</u>	<u>R. basiola</u>	<u>R. striatella</u>	<u>R. fausta</u>
n	10	13	10	10	10
HL	.68±.016 (.59-.73)	.74±.032 (.65-.78)	1.18±.028 (.97-1.26)	1.24±.047 (1.17-1.32)	.86±.025 (.81-.94)
HW	1.14±.024 (.95-1.21)	1.23±.001 (1.11-1.34)	1.70±.036 (1.41-1.83)	1.72±.022 (1.60-1.85)	1.28±.026 (1.11-1.37)
HH	.93±.033 (.75-1.06)	1.04±.024 (.90-1.19)	1.46±.039 (1.20-1.69)	1.61±.022 (1.53-1.74)	1.08±.023 (.95-1.15)
EW	.57±.010 (.51-.61)	.61±.009 (.52-.67)	.82±.018 (.68-.88)	.81±.010 (.76-.87)	.63±.013 (.55-.67)
EH	.76±.019 (.66-.82)	.83±.015 (.62-.92)	1.16±.030 (.94-1.27)	1.25±.017 (1.15-1.33)	.88±.020 (.77-.95)
FrWV	.44±.017 (.33-.50)	.46±.009 (.35-.51)	.65±.010 (.58-.69)	.73±.009 (.68-.78)	.46±.010 (.41-.51)
AL	.36±.006 (.31-.38)	.36±.001 (.32-.39)	.54±.008 (.48-.57)	.59±.010 (.53-.63)	.43±.011 (.37-.47)
FL	.52±.013 (.43-.56)	.57±.007 (.49-.64)	.79±.026 (.60-.90)	.99±.020 (.90-1.14)	.54±.029 (.50-.62)
GW	.17±.008 (.13-.22)	.18±.001 (.13-.20)	.23±.001 (.22-.27)	.35±.008 (.31-.38)	.18±.008 (.15-.23)
TL	1.30±.048 (1.01-1.52)	1.44±.028 (1.26-1.60)	2.44±.067 (2.05-2.70)	2.29±.032 (2.17-2.46)	1.70±.042 (1.44-1.82)
n	10	17	10	10	10
WL	2.34±.040 (2.05-2.44)	2.56±.028 (2.32-2.78)	4.41±.096 (3.75-4.73)	3.93±.052 (3.71-4.20)	3.28±.090 (3.00-3.65)
WW	1.14±.025 (.99-1.24)	1.40±.018 (1.28-1.50)	1.97±.050 (1.60-2.13)	1.94±.025 (1.82-2.06)	1.51±.036 (1.34-1.70)

Table 12A. Body and wing measurements of males of the ribicola species group and miscellaneous species. Figures represent mean, standard error, and range.

	<u>R. ribicola</u>	<u>R. berberis</u>	<u>R. basiola</u>	<u>R. striatella</u>	<u>R. fausta</u>
n	10	13	10	10	10
HL	.76±.016 (.61-.79)	.82±.016 (.70-.89)	1.22±.026 (1.07-1.34)	1.33±.028 (1.16-1.43)	.93±.015 (.85-1.00)
HW	1.21±.024 (1.02-1.32)	1.36±.029 (1.19-1.49)	1.78±.036 (1.53-1.91)	1.87±.033 (1.64-1.96)	1.43±.029 (1.22-1.51)
HH	.99±.023 (.84-1.12)	1.15±.023 (.97-1.28)	1.47±.038 (1.23-1.62)	1.73±.040 (1.50-1.86)	1.17±.021 (1.02-1.27)
EW	.62±.013 (.53-.69)	.68±.014 (.57-.75)	.87±.032 (.76-.93)	.85±.017 (.72-.91)	.70±.016 (.60-.76)
EH	.82±.018 (.68-.90)	.93±.019 (.78-1.01)	1.24±.031 (1.03-1.35)	1.35±.023 (1.19-1.46)	.97±.020 (.82-1.04)
FrWV	.48±.013 (.39-.54)	.52±.012 (.44-.56)	.66±.018 (.59-.78)	.80±.018 (.69-.87)	.49±.025 (.45-.54)
AL	.39±.009 (.33-.41)	.41±.001 (.36-.46)	.56±.012 (.50-.62)	.62±.011 (.56-.68)	.47±.008 (.42-.52)
FL	.55±.008 (.49-.58)	.66±.013 (.57-.70)	.82±.019 (.70-.90)	1.07±.032 (.86-1.20)	.59±.027 (.55-.64)
GW	.18±.005 (.15-.22)	.21±.014 (.16-.27)	.22±.001 (.17-.27)	.38±.015 (.31-.46)	.18±.006 (.15-.21)
TL	1.43±.050 (1.08-1.54)	1.63±.044 (1.35-1.83)	2.62±.064 (2.21-2.85)	2.69±.065 (2.27-2.87)	1.99±.046 (1.65-2.13)
n	10	12	11	11	11
WL	4.00±.079 (2.75-3.38)	2.86±.069 (2.39-3.09)	4.80±.076 (4.19-5.14)	4.79±.068 (4.43-5.08)	3.60±.100 (3.09-4.15)
WW	1.47±.038 (1.27-1.62)	1.58±.041 (1.31-1.73)	2.27±.051 (1.90-2.59)	2.34±.043 (2.07-2.51)	1.74±.056 (1.50-2.06)

Table 12B. Body and wing measurements of females of the ribicola species group and miscellaneous species. Figures represent mean, standard error, and range.

male, and II-V in female as in *tabellaria* (Figs. 57-58). *Genitalia: male*—epandrium (Figs. 84, 104) black; surstyli yellow, straight; phallic apodeme sharply curved and flared apically; ejaculatory apodeme (Fig. 147) with heavily sclerotized keel along apical end; aedeagus (Fig. 127) with setulose apical appendage; vesica not well developed. *Female*—variation in ovipositor length shown in Figure 17; ovipositor with two minute preapical setae; ovipositor sheath shining black. Three spermathecal ducts and two twisted cylindrical spermathecae (Fig. 167) sparsely covered with scale-like papillae.

Chromosome number and morphology (Fig. 228). The diploid number in both sexes is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No secondary constrictions or morphologically differentiated heterochromosomes (XY) were observed.

Source of cytological material: *Ribes* spp., Burns, Harvey Co., Oregon, 4199 ft., July 28, 1961.

Courtship behavior. This species was not studied under field conditions. In the laboratory, males readily courted females without the presence of host fruit. It is therefore not known if *ribicola* males are territorial. In plastic observation chambers, males would actively court females with a characteristic wing flicking consisting of a rapid forward movement followed by a rapid upward jerk. The male, upon sighting the female, rapidly turns in her direction. This movement is usually followed by several wing flicking movements to which the female responds with a similar, but not identical, rapid wing movement. The male then crouches and slowly stalks the female, weaving back and forth as he moves. Upon reaching the female, but without touching her, he flies onto her back and attempts copulation. If the female is ready to mate she spreads her wings, lifts her abdomen, and extrudes her ovipositor. No licking or tapping which has been reported for many

Drosophila (Spieth, 1952) was ever seen in the courtship of *ribicola*. Males would actively court females through a plastic partition, but would not court males. This indicates that the male is capable of recognizing the female on strictly visual cues without the use of pheromones.

Hosts. *R. ribicola* has been reared from both wild and cultivated currants and gooseberries, including *Ribes aureum* Pursh (Phillips, 1946), *R. grossularia* L. and *R. vulgare* (Piper and Doane, 1898). This species seems to limit itself strictly to members of the genus *Ribes* (Saxifragaceae). A single specimen of *ribicola* from Guadalupe, California, bearing a label "ex strawberry," probably was not reared from this fruit. The same seems to be true of a specimen of *berberis* bearing the same locality, date, and host record. Both specimens appear to have spent some time in a McPhail trap, although there are no labels to this effect. They are covered with a white film typical of insects removed from a liquid trap using fermenting lure.

The host relationships of this species are so poorly known that no attempt was made to plot the distribution of the individual species of *Ribes*. Map 10 shows the general distribution of *Ribes* spp. in North America and gives some idea of the distribution of *ribicola* in relation to its potential host species.

Distribution (Map 10). **CANADA:** BRITISH COLUMBIA: Lillooet. **U.S.A.:** IDAHO: Moscow, Latah Co. WYOMING: Big Horn Co. WASHINGTON: Washington Expt. Stations No. 020, No. 66; Chehalis, Lewis Co.; Opportunity, Spokane Co. OREGON: Burns, Harvey Co. CALIFORNIA: Guadalupe, Santa Barbara Co.

Note on California distribution. All of the California specimens referred to *ribicola* by Foote and Blanc (1963) that I have examined are *juniperina* and are treated with that species. Specimens of *ribicola* recorded by Foote and Blanc from the following localities were not examined: Woodfords, Alpine Co.; Echo Lake, El Dorado



Co.; Tioga Pass, Mono Co.; Dunsmuir, Siskiyou Co.; Mineralking, Tulare Co.; Dardanelles, Tuolumne Co. The only record of *ribicola* in California that I have been able to definitely establish on purely morphological grounds is the single male from Guadalupe. Chromosomes studied from larvae removed from the fruit of *Ribes* spp. near McCloud, Siskiyou Co., California on Aug. 2, 1961, proved to be different from those of *ribicola* in both morphology and number ($2n=10$ vs. $2n=12$ for *ribicola*). The larvae were probably those of *Epochra canadensis* (Loew), a species which occurs over most of California (Foote and Blanc, 1963). Adults were not reared from this collection.

Rhagoletis berberis Curran

Rhagoletis berberis Curran, 1932, Amer. Mus. Nov., 526: 6, 8. [Holotype examined: ♀, Hood River, Oregon, June 23, 1931, *Berberis nervosa* Pursh. (AMNH); ♂ allotype, Hood River, Oregon, July 30, 1930 (AMNH); 3 ♂ ♂ paratypes, same data as allotype.] —Pickett, 1937, Canad. J. Res. (D), 15: 60 (genitalia). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 26, 61–62, figs. 20, 65, 120, 121, 167 (larval morphology, in key).

Diagnosis. The entirely black body, characteristic wing pattern (Fig. 202), genitalia (Figs. 87, 106, 126, 149), and karyotype (Figs. 229–230) make it easy to distinguish this species from all other North American representatives of *Rhagoletis*. The apical band of the wing is contiguous with the costa and not separated from it by a hyaline region as in *ribicola* and members of the *tabellaria* group. *R. berberis*, with a karyotype consisting of 12 autosomes and a heteromorphic sex chromosome pair, is the only member of the genus *Rhagoletis* thus far studied with a diploid number of 14.

Description. Body and wing measurements in Tables 12A–12B. **Head** (Fig. 35): posterior region dark brownish black to black except for yellow upper occiput and dark cream postorbital region. Frons and antennae yellow, parafacialia and face cream to white; parafacialia and genae

light yellow, latter grading to white posteriorly; occasional individuals may have these areas slightly tinted with red; mentum black. Genal and postocellar bristles yellowish brown to black; all other major bristles, including single intravertical and 5–9 postorbitals, black; gular bristles not differentiated from rest of light yellow bristles on postgenae and gulamentum. **Thorax:** black; mesonotum with four rows of yellow decumbent setae and white pollinose microtrichia similar to that of *tabellaria* (Fig. 46); inner row shorter than outer row, latter broken at transverse sulcus. Dorsocentrals slightly before a line drawn between anterior supraalars; two mesopleural bristles. Notopleural stripe and scutellar spot cream tinted with yellow, latter reaching anteriorly from below apex to a line drawn between basal scutellars; lateral margins passing outside base of apical scutellars. Postscutellum shining black; halteres cream grading to light yellow at base, or entirely light yellow. **Legs:** coxae, trochanters, and femora brownish black, latter yellow at apices. Tibiae I and II yellow, Tibia III brownish black, slightly bowed with row of stout semierect setae on anterior outer surface. All tarsal segments yellow. **Wing** (Fig. 202): medial band not reaching posterior margin and not joined to basal or subapical crossbands. Apical band contiguous with costa over entire length. R_{4+5} bare, with a seta dorsally at junction with R_{2+3} . Crossvein r-m about midway between m and M_3 . Anal cell bluntly pointed (Fig. 177). **Abdomen:** all segments black with white pollinose band along posterior margin of tergites II–IV in both sexes, some females with narrow white band on posterior margin of tergite V as in *tabellaria* (Figs. 57–58). **Genitalia:** male—epandrium black; surstyli yellow, tapering to sharp point (Figs. 87, 106); dorsal margin of surstyli serrated near base; phallic apodeme straight, aedeagus with long apical appendage covered at tip with short setae (Fig. 126); vesica hood-like; ejaculatory apodeme normal

(Fig. 149). *Female*—variation in ovipositor length shown in Figure 17; ovipositor with two minute preapical setae; ovipositor sheath shining black. Two spermathecal ducts and two cylindrical spermathecae covered with only a few scattered scale-like papillae (Fig. 166).

Chromosome number and morphology (Figs. 229–230). The diploid number is 14; the MCA number is 23 in the male and 24 in the female. The male karyotype consists of four pairs of metakinetic autosomes and two pairs of acrokinetic autosomes, as well as a metakinetic X and an acrokinetic Y dot sex chromosome. In the female karyotype there are four pairs of metakinetic autosomes, two pairs of acrokinetic autosomes, and a single pair of metakinetic X chromosomes. The acrokinetics were verified through the study of late metaphase and early anaphase figures in which the kinetichores were just beginning their advance to the poles. A secondary constriction was always noted at metaphase in the short arm of the longest metakinetic autosome (Figs. 229–230).

Source of cytological material: *Mahonia nervosa*, Shaw, Oregon, 22 July 1961.

Courtship behavior. Males of *berberis* were frequently seen patrolling berries of Oregon grape, which suggests that this species, like many other *Rhagoletis*, is territorial, and courtship probably occurs on or near fruit of the host plant.

Hosts. *R. berberis* has been reared from *Mahonia nervosa* (Pursh) Nutt. (Berberidaceae) or Oregon grape (Curran, 1932), which occurs in the coniferous forest and humid transition zone from Vancouver Island, British Columbia, to Monterey, California. I have also examined specimens reared from *Mahonia aquifolium* (Pursh.) Nutt. A single specimen from California bearing the label "ex strawberry" is probably an error. It appears to have been taken in a liquid bait trap (for details see *ribicola*, *Hosts*). There are several other species of native northwestern *Mahonia* which may also serve as hosts for *berberis*.

The host relationships of *berberis* are too poorly known to reach any definite conclusions about its origin, though like *ribicola*, it seems to be more closely related to Eurasian *Rhagoletis* such as *berberides* Benedek and possibly *cerasi* (*sensu lato*), both of which infest *Mahonia*. The present distribution of *berberis* and its association with *M. nervosa* suggest that it is probably a recent arrival from eastern Asia. *M. nervosa* is the only representative of the *Orientales* group (Section *Longibracteatae*) in the Western Hemisphere, a group restricted to southeastern Asia (Ahrendt, 1961). A careful search for related species of *Rhagoletis* infesting *Berberis* and *Mahonia* in eastern Asia could help to establish the origin and affinities of *berberis*.

Distribution (Map 11). **CANADA:** BRITISH COLUMBIA: Langford; Robson; Summerland; Vancouver. **U.S.A.:** WASHINGTON: N. Bonneville, Skamania Co.; Wenatchee, Chelan Co.; Puyallup and La Grande (Univ. of Wash. Demonstration Forest), Pierce Co.; Kettle Falls, Stevens Co.; Walla Walla, Walla Walla Co.; Seattle, King Co.; Juniper Beach; Glen Elum. OREGON: Hood River, Hood River Co.; Corvallis, Benton Co.; Shaw, Macleay, Marion Co. CALIFORNIA: Susanville, Lassen Co.; Etna, Dunsmuir, Horse Creek, Happy Camp, Yreka, Siskiyou Co.; Guadalupe, Santa Barbara Co.

MISCELLANEOUS SPECIES

Rhagoletis basiola (Osten Sacken)

Trypeta flavonotata,¹⁸ —Loew, 1873, Smithsonian Misc. Coll., 256: 244 (Yukon River, Alaska). —Coquillett, 1899, J. New York Ent. Soc., 7: 261 (syn. *Zonosema basiolum* and *Spilographa setosa*).

Trypeta (*Zonosema*) *basiolum* Osten Sacken, 1877, U.S. Geol. and Geogr. Survey Bull., 3: 348. [Cotypes examined: ♀, lectotype by present designation, Brookline, Mass. (MCZ, No. 10244); ♀, Collins, Idaho, 27 July 1898 (J. M. Aldrich Coll.) (USNM, No. 43546; MCZ, No. 17081).]

Spilographa setosa Doane, 1899, J. New York

¹⁸ *Trypeta flavonotata* Macquart is synonymous with *Zonosemata electa* (Say) (see Stone, 1951).



Ent. Soc., 7: 178–179, pl. 3, fig. 1. [Cotypes examined: ♀, Vollmer, Idaho, 31 July 1898 (USNM, No. 43546), designated lectotype by Stone, 1951; ♂, Pullman, Wash., 2 Aug. 1898 (AMNH, No. 16113).]

Spilographa basiolium. —Aldrich, 1905, *Smithson. Misc. Coll.*, 46: 604.

Zonosema flavonotata. —Phillips, 1923, *J. New York Ent. Soc.*, 31: 128, pl. 28, fig. 9 (in key, distribution; = *Zonosema basiolium* Osten Sacken).

Zonosema setosa. —Phillips, 1923, *J. New York Ent. Soc.*, 31: 128, pl. 28, fig. 10 (in key, distribution). —Benjamin, 1934, *U.S. Dept. Agr. Tech. Bull.*, 401: 18 (discussion of synonymy).

Zonosemata setosa. —Phillips, 1946, *Mem. Amer. Ent. Soc.*, 12: 98–100, figs. 45, 87, 192 (larval morphology, in key).

Rhagoletis basiola. —Stone, 1951, *Proc. Ent. Soc. Wash.*, 53: 45–48 (nomenclatorial history). —Balduf, 1959, *Illinois Biol. Monogr.*, 26: 1–194 (biology, description).

R. basiola is the only representative in the Western Hemisphere of the *alternata* species group, which includes five described Eurasian species. Species in this group infest the fruits of *Rosa* (Rosaceae), *Berberis* (Berberidaceae), and *Lonicera* (Caprifoliaceae). Some authors have considered the *alternata* group to represent a distinct genus (Loew, 1862; Collin, 1947; Rohdendorf, 1961) (see Introduction for details).

R. basiola is most closely related to *alternata*, and until recently they were considered conspecific. Stone (1951), however, found consistent differences between the Palearctic and Nearctic populations, and concluded that they should be regarded as distinct species. He has also presented a résumé of the nomenclatorial history of this species.

Certain morphological characters of *basiola*, such as light body coloration, wing pattern, and position of dorsocentral bristles, suggest a possible relationship with both South American *R. ferruginea* Hendel and the Nearctic genus *Zonosemata* Benjamin.

Diagnosis. *R. basiola* is distinguished from *alternata* in having the apical wing band usually joined to the subapical cross-band (Fig. 212). In *alternata*, these two

bands are usually separated (Fig. 208). The pattern of the postscutellum also offers a useful character for the separation of the two species. In *basiola*, there are two highly variable, small, circular or triangular-shaped dark brown spots (Figs. 173–174) with their broad bases on the dorsal margin of the postscutellum and ending on or near the lower margin. The bands on the postscutellum of *alternata* are broad, never triangular-shaped (Fig. 175), and are much wider than the medial yellow stripe.

Description. Body and wing measurements in Tables 12A–12B. Entirely yellow species, except for dark brown markings on postscutellum, fuscous wing bands, and distinct black spot on mesonotum just above base of wing. **Head** (Fig. 38): posterior surface light yellow; antennae and frons darker yellowish orange; face and genae yellowish white; mentum yellow. All major head bristles light brown to yellow; 1–2 postverticals, 7–14 postorbitals. **Thorax:** all regions including scutellum light yellow except for lighter cream-colored notopleural stripe; scutellum without scutellar spot; postscutellum with two variable black circular or triangular spots (Figs. 173–174) usually beginning broadly along dorsal margin of postscutellum and ending on or well before lower margin. Dorsum covered with yellow decumbent setae and yellow pollinose microtrichia not arranged in definite pattern; two pairs yellow scapular bristles, sometimes individually doubled with smaller second bristles located in tandem behind primary bristles; major bristles generally brownish black to brown; dorsocentrals well behind anterior supraalars, but slightly closer to anterior supraalars than anterior pair of posterior supraalars; two mesopleural bristles of about equal size. **Legs:** all segments light yellow. Tibia II with distinct row of five to six semierect stout setae along outer posterior margin; tibia III with row of well developed semierect setae on outer anterior surface. **Wing** (Fig. 212): pattern similar to that of *Zonosemata electa* and to several European

species in *alternata* group. Basal band narrow, medial band not reaching posterior margin of wing and not joined to either weakly developed basal or well developed subapical bands; stigma more heavily infuscated than rest of medial band; small triangular-shaped intercalary band beginning on costa about midway between apical and subapical bands, reaching posteriorly and ending on or near vein R_{4+5} ; apical band usually joined to subapical band though somewhat narrowed at junction in most specimens; occasional individuals with these bands separated by hyaline area. R_{4+5} setulose with 1–3 setae at junction with R_{2+3} . Crossvein r-m slightly closer to M_3 than to m. Anal cell pointed. *Abdomen*: all segments yellowish tan, slightly darker than thorax. *Genitalia: male*—epandrium and surstyli yellowish tan, latter tapering beyond prenisetae to sharp point; phallic apodeme curved (Figs. 88, 96). Aedeagus (Fig. 128) with small finger-like apical appendage; vesica smooth. Ejaculatory apodeme normal (Fig. 139). *Female*—variation in ovipositor length shown in Figure 19; ovipositor short and broad, wider at middle than at base; ovipositor with two minute preapical setae; ovipositor sheath brownish orange. Three spermathecal ducts and two (rarely three) globular spermathecae covered with appressed, sharply pointed scale-like papillae (Fig. 169).

Geographical variation. No geographical variation was noted in the morphology of this species.

Chromosome number and morphology (Figs. 231–233). The diploid number in both sexes is 10; the MCA number is 18 as in anaphase there are five pairs of meta-kinetic or submetakinetic chromosomes, two pairs of which have very short, almost subtelokinetic arms (Fig. 231). In late prophase or early metaphase plates the large satellites that are so prominent in metaphase (Fig. 233, SAT) are often separated from the long arms of the chromosomes by a nucleolus, giving the appear-

ance of the karyotype typical of other *Rhagoletis* species. At first glance, the two satellites in this case appear as two dot chromosomes which, when counted as such, give a diploid number of 12. In anaphase (Fig. 232) the positions of the kinetocore can be readily localized.

A distinct difference between the length of the arms of the longest chromosome pair was noted in anaphase configurations of some specimens. This heteromorphic chromosome pair probably represents the sex chromosome (Fig. 232).

Source of cytological material: *Rosa* spp., Lincoln, Mass., various dates in Sept. 1962.

Courtship behavior. I have not observed the courtship of this fly under laboratory or natural conditions. Balduf (1959) states that males are usually more conspicuous than females, mostly confining themselves to the undersides of leaves and the hips which indicates that this species may use the host fruit as a rendezvous for courtship. The flies apparently mate readily under laboratory conditions (Balduf, 1959), although I was unable to observe copulation in the few specimens I reared from Lincoln, Mass., and those sent to me from Minnesota by Dr. Balduf.

Parasites. Balduf found four species of hymenopterous parasites attacking the immature stages of *basiola*. One of these is known only from the larval stage, and Balduf tentatively identified it as a eupelmid (probably *Eupelmus* sp.). Two others, *Opius rosicola* Muesebeck and *O. baldufi* Muesebeck (Braconidae), occur sympatrically and are widely distributed over northern North America. *Halticoptera rosae* Burks (Pteromalidae), an egg parasite, has also been reared frequently from *basiola*.

Hosts. Balduf (1959) recently summarized the ecology of *R. basiola* and the closely related European species, *R. alternata*. It is through his efforts that so much is known about this species today.

A total of 19 species of *Rosa* have been recorded as hosts of *R. basiola*. These are listed in Table 13 with the localities in

TABLE 13. SPECIES OF *Rosa* FROM WHICH *R. basiola* HAS BEEN REARED. (FROM BALDUF, 1959)

<i>Rosa</i> spp.	<i>Locality</i>
<i>R. acicularis</i> Lindl.	N Canada, Alaska, NE Minn.
<i>R. alcea</i> Greene	B.C., Sask., Man.
<i>R. arkansana</i> Porter	Wisc.
<i>R. blanda</i> Ait.	NE Minn., Wisc., Ont.
<i>R. canina</i> L.	Ohio, Ind., Ill.
<i>R. carolina</i> L.	Wisc., Ohio, Ind., Ill.
<i>R. eglanteria</i> L.	N.C.
<i>R. gallica</i> L.	Ohio, Ind., Ill.
<i>R. macounii</i> Greene	NE Minn., B.C., Sask., Man., Neb.
<i>R. nitida</i> Willd	Maine
<i>R. nutkana</i> Presl.	B.C., Sask., Man., NW United States
<i>R. palustris</i> Marsh.	Ohio, Ind., Ill.
<i>R. pyrifera</i> Rydl.	B.C., Sask., Man.
<i>R. rugosa</i> Thund	R.I., N.Y.
<i>R. setigera</i> Michx.	Ohio, Ind., Ill.
<i>R. spaldingii</i> Crepin	NW United States
<i>R. ultramontana</i> (S. Wats.) Heller	NW United States
<i>R. virginiana</i> Mill.	Maine
<i>R. woodsii</i> Lindl.	B.C., Sask., Man., Utah

which they were collected. Balduf noted a considerable variation in the number of larvae per unit number of rose hips correlated with the latitude in which they were collected.

There was a steady decline in the ratio of larvae to hips from the northern to southern limits of the range, averaging 40–54 per cent in Ely, Minnesota, and only 4 per cent in central Illinois with some large samples completely devoid of infestation.

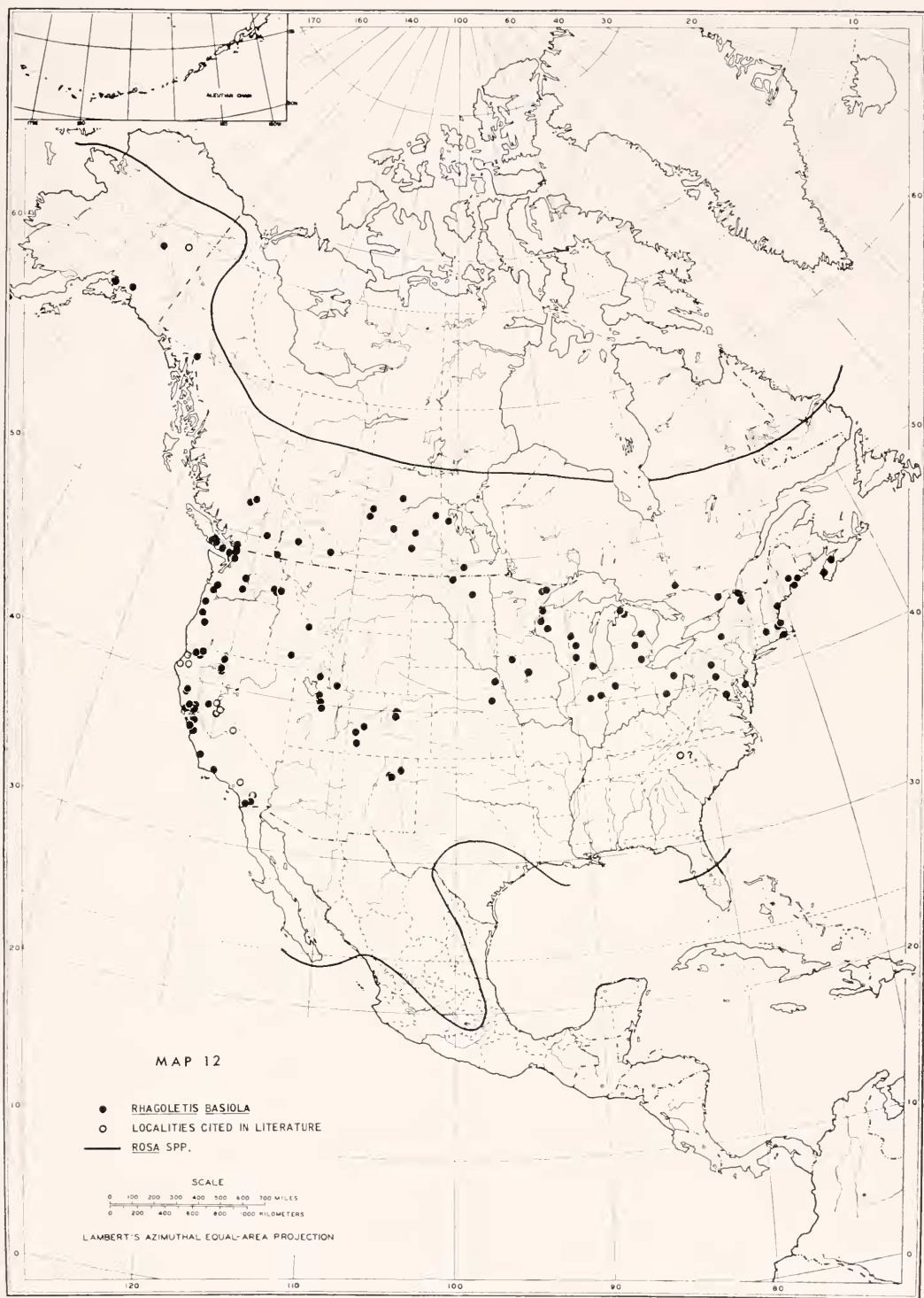
Distribution (Map 12). *R. basiola* has the widest range of any North American representative of *Rhagoletis*. Apparently it is better adapted to the cold temperate regions, occurring wherever favorable climatic conditions and suitable species of *Rosa* exist. The most northerly record is Miller House, 66 miles south of the Arctic Circle. Balduf (1959, p. 25) had no records of *basiola* south of latitude 35° N, but its presence in southern California at 35° 5' (see Map 12) indicates that this species is capable of adjusting to rather moderate conditions of mild winters.

Rhagoletis striatella van der Wulp

Rhagoletis striatella van der Wulp, 1899, Biol. Cent. Amer., Dipt., 2: 408–409, tab. XI, fig. 30. [Type not examined, location unknown; ♀, Amula (now Amulango), Guerrero, Mexico.] —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 7, 14 (in key, description). —Phillips, 1923, J. New York Ent. Soc., 31: 135–136, pl. 18, fig. 27 (in key). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 405–406, pl. 16, fig. 3 (redescription, wing figured). —Curran, 1932, Amer. Mus. Nov., 526: 6 (in key). —Aczél, 1954, Dusenya, 5: 78 (in key).

Diagnosis. *R. striatella* is probably the most distinctive member of the genus in North America. Its extremely long ovipositor, broad genae, bulging postgenal regions, and wing pattern ally it closely to no other Holarctic species. It is more closely related to some of the South American species, such as *R. lycopersella*, *psalida*, and *ochraspis*, but differs from all described species of *Rhagoletis* in having a V-shaped scutellar spot, and two broad white pollinose stripes on the dorsum (Fig. 42). The wing pattern of *striatella* (Fig. 209), with the subapical band joined to the forked apical band forming the letter F, also serves to identify this species. Superficially, this pattern resembles that of *fausta* (Fig. 210), except that in *fausta* the subapical band is joined to the medial band. In *striatella*, these two bands are separated by a hyaline area.

Description. Body and wing measurements in Tables 12A–12B. *Head* (Fig. 41): posterior surface yellow; frons bright yellow; antennae more yellowish orange; face light yellow, covered with white pollinose microtrichia; genae yellow, postgenae and postorbital regions a lighter whitish yellow; mentum brownish black, haustellum heavily shaded with black. Genae with black setae along ventral margins and with a black shaded spot below eye; genal bristle yellow, all other major bristles black; gular bristle not differentiated from black to yellow setae on postgena and gulamentum; 1–5 intraverticals; 2–5 postverticals; 11–23 postorbitals. Three to four lower fronto-



orbital bristles, variable. *Thorax* (Fig. 42): black except for cream colored notopleural stripe and V-shaped scutellar spot; post-scutellum black; halteres light lemon yellow, slightly darker at base. Dorsum covered with yellow to black decumbent setae and white pollinose microtrichia, latter arranged in two broad rows; usually two pairs of scapular bristles, sometimes individually doubled with second smaller bristles in tandem behind first; dorso-centrals slightly behind anterior supracrals; two mesopleural bristles. *Legs*: coxae black; femora black except for yellow knees. All trochanters and tibiae I and II yellow, heavily shaded with black. Tibia III black. Tarsi dark yellow. *Wing* (Fig. 209): medial band not reaching hind margin nor joined to basal or subapical bands. Subapical band joined to forked apical band forming an F-shaped pattern. R_{4+5} with many setae on dorsal surface, occasionally with one or two on ventral surface. One to two setae dorsally at junction of R_{4+5} and R_{2+3} . Anal cell pointed. Crossvein r-m at midpoint between m and M_3 . *Abdomen*: base color black with tergites polished. Tergites II–IV in male, and II–V in female with white pollinose band along posterior margin. *Genitalia*: male—epandrium black; surstyli short and broad, yellow (Figs. 89, 105); hypopygium elongated; genital ring membrane with well developed pouch; fultella with a broad shelf behind base of phallic apodeme. Aedeagus (Fig. 134) long and narrow, with a long apical finger-like appendage; vesica smooth. Ejaculatory apodeme normal, heavily pigmented (Fig. 140). *Female*—variation in ovipositor length shown in Figure 19; ovipositor long compared with other *Rhagoletis* species (Figs. 17–21, 182–183), with a distinct subapical constriction (Fig. 184); ovipositor sheath shining black; two long preapical setae. Two spermathecal ducts; two globular spermathecae (Fig. 170) with small pointed appressed scale-like papillae. Base of spermatheca cylindrical; apex with nipple-like protuberance.

Egg. The egg of this species is not typical of other *Rhagoletis* species. The end bearing the micropyle is elongated rather than blunt as in all other species (Figs. 240–241).

Chromosome number and morphology (Figs. 234–235). The diploid number in the male is 11, and in the female 12. In this species there is a compound sex-determining mechanism consisting of a long acrokinetic X_1 , a shorter acrokinetic X_2 bearing a distinct satellite, and a long acrokinetic, or possibly subacrokinetic, Y chromosome which is shorter than X_1 but longer than X_2 . In addition to the heteromorphic sex chromosomes, there are three pairs of metakinetic autosomes and a single pair of acrokinetic autosomes. Therefore, the MCA number in the male is 17, and in the female 18. Other than the satellite on the X_2 , no other secondary constrictions were noted.

The remaining pair of short autosomes are acrokinetic. The dot chromosomes, normally present in other *Rhagoletis* species, are not found in *striatella*. The satellites of the X_2 sex chromosomes, occasionally separated from the parent chromosomes during squashing, may be confused with dots in the karyotype of the female. Only one dot is present in the karyotype of the male.

Source of cytological material: *Physalis* sp., El Yukon, Mex., Mexico, 8,800 ft., Aug. 4, 1962.

Hosts. The first host record for *striatella* resulted from an interception by the U.S. Department of Agriculture at Brownsville, Texas, of infested husk tomatoes (*Physalis* sp., Solanaceae) from Mexico. *R. striatella* is reputed to cause considerable damage to cultivated husk tomatoes in Mexico, although its economic importance as a pest has not been documented. The distribution of this species over much of central United States, southern Canada, and Mexico indicates that *striatella* probably infests several species of *Physalis* in different parts of its range.



Distribution (Map 13). **CANADA:** ONTARIO: Chatham. **U.S.A.:** MICHIGAN: Agr. Coll. Mich., East Lansing, Ingham Co. WISCONSIN: Deer Co. ILLINOIS: Algonquin, McHenry Co. IOWA: vicinity of Gilbert, Story Co. NEW MEXICO: Las Vegas, San Miguel Co. TEXAS: Eagle Pass, Maverick Co. **MEXICO:** TLAXCALA: Huamantla. MEXICO: vicinity of Agua Bendita; Tenango de Valle; El Yukon. GUERRERO: Amulango (formerly Amula).

Rhagoletis fausta (Osten Sacken)

Trypeta (*Acidia*) *fausta* Osten Sacken, 1877, U.S. Geol. and Geogr. Survey Bull., 3: 346. [Syn-types examined: ♀, lectotype by present designation, Mt. Washington, N.H., Alpine No. 1332 (Geo. Dimmock) (Osten Sacken Coll.; MCZ, No. 10234); ♀, same locality and collector as lectotype, Alpine No. 1331.]¹⁹

Rhagoletis fausta, —Coquillett, 1899, J. New York Ent. Soc., 7: 260 (syn. *Acidia fausta*). —Aldrich, 1910, Canad. Ent., 42: 99–100 (synonymizes *intrudens* with *fausta*). —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 19 (note, in key). —Phillips, 1923, J. New York Ent. Soc., 31: 135–136, pl. 28, fig. 26 (in key, note). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 404–405, pl. 14, fig. 2 (in key, re-description). —Curran, 1932, Amer. Mus. Nov., 526: 6 (in key). —Pickett, 1937, Canad. J. Res. (D), 15: 61 (genitalia). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 66, figs. 23, 68, 125, 126, 170 (larval morphology, in key).

Rhagoletis intrudens Aldrich, 1909, Canad. Ent., 41: 70, 72, pl. 4, fig. 3. [Type examined: ♀, Victoria, B.C., 6.3142, W. R. Palmer, emerged at Ottawa, 19.VI.1907 (USNM, No. 42214).]

There are two allopatric populations of *fausta* in North America (Map 14). No morphological differences could be found between these two populations which are confined to the northeastern and northwestern regions of the continent. In the absence of crossbreeding experiments, it is best to consider the two populations as

one species although they utilize different species of *Prunus* as hosts.

Diagnosis. *R. fausta* is easily distinguished from all other *Rhagoletis* by its characteristic wing pattern (Fig. 210) and the absence of white bands along the posterior margin of the abdominal tergites.

The only species with which *fausta* bears some resemblance is the female of the European leafminer, *Philophylla heraclei* Linnaeus, which has a similar wing pattern and general habitus. The position of cross-vein r-m, the absence of a hyaline spot in cell R₃, black markings on the posterior region of head and legs, as well as the white scutellar spot, will easily distinguish *fausta* from *heraclei*. The male of *P. heraclei* is almost entirely yellow and resembles the male of *fausta* only in wing pattern.

The exact relation of *fausta* to other members of the genus *Rhagoletis* is uncertain. The globular spermathecae and apical F-shaped pattern of the wing show some similarity to *striatella*. However, the wide distribution of *fausta* in the northern cold temperate region, and its limitation to higher altitudes as it moves southward, indicate that this species is probably not of tropical origin. Its relationships will therefore have to remain in doubt until both the Asiatic and Neotropical representatives of the genus are better known.

Description. Body and wing measurements in Tables 12A–12B. *Head* (Fig. 40): posterior surface black. Postorbital, upper one-third of occiput, frons, antennae, and palps golden yellow; face, genae, and anterior margin of postgenae yellow to whitish yellow; mentum black. Postocellar, gular, and genal bristles yellow; all other major bristles, including single postvertical and 7–14 postorbitals, black; occasional specimens with four pairs of lower fronto-orbital bristles. *Thorax*: black except for yellowish white concolorous scutellum and notopleural stripe, latter with black shading only along lateral margins near base; post-scutellum brownish black; halteres lemon

¹⁹ Osten Sacken's original description refers to a male and a female as cotypes. Both specimens bearing type labels in the MCZ collection are females.

yellow. Dorsum covered with brownish black decumbent setae and diffuse white pollinose microtrichia arranged in four ill-defined broad rows; in some specimens medial rows more distinct than outer rows; dorsocentrals slightly before anterior supralars; one well developed mesopleural with smaller, lower bristle present in most specimens; pteropleural bristle reduced, sometimes minute, usually one-third length of upper mesopleural bristle. *Legs*: coxae and femora dark brownish black; trochanters, all tibiae, and tarsal segments yellow. Tibiae II and III may bear light to heavy brown shading, particularly on posterior surface. *Wing*: pattern as in Figure 210; R_{4+5} bare except for single seta on dorsal surface of junction with R_{2+3} . Medial band broadly joined to subapical band in cell 1st M_2 ; large hyaline spot in subapical band just apicad of junction; apical band forked, similar to that of *striatella*. Crossvein r-m about midway between m and M_3 . Anal cell pointed. *Abdomen*: all segments in both sexes entirely black, without white band along posterior margin. *Genitalia*: *male*—epandrium black, surstyli yellowish orange (Figs. 74, 110); phallic apodeme curved; genital ring membrane normal. Aedeagus (Fig. 117) without apical appendage; vesica smooth. Ejaculatory apodeme normal (Fig. 151). *Female*—variation in ovipositor length shown in Figure 19; ovipositor tip with two minute subapical setae; ovipositor sheath black. Three spermathecal ducts, two globular spermathecae (Fig. 171) covered with appressed scale-like papillae.

Chromosome number and morphology (Figs. 236–237). The diploid number in both sexes is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. At metaphase, a secondary constriction is sometimes present on one pair of submetakinetic chromosomes (Fig. 236), and a distinct satellite is always clearly visible at metaphase in a second pair of submetakinetic chromosomes (Fig.

236). No morphologically differentiated heterochromosomes (XY) were observed.

Source of cytological material: *Prunus pennsylvanica*, Blue Hills, vicinity Canton, Mass., 300 ft., July 4, 1963. *P. emarginata*, Blue Canyon Airport, Placer Co., California, 5,200 ft., Aug. 9, 1961.

Courtship behavior. The courtship behavior of this species was not studied.

Parasites. Middlekauff (1941) and Frick et al. (1954) found the following hymenopterous parasites attacking *fausta*: *Pachycrepoides dubius* Ashmead (Pteromalidae); *Tetrastachus faustus* Burks (Eulophidae); *Eucoil* sp. (Cynipidae); *Phygadeuon epochrae* Viereck (Ichneumonidae).

Hosts. Details of the host relationships of this species have been discussed by Frick et al. (1954). *R. fausta* was recorded infesting cultivated cherries in British Columbia by Aldrich (1909), who incorrectly named it *R. intrudens*. In 1910 he recognized his error and synonymized his own species with *fausta*. Soon afterward, Illingworth (1912) reported that *fausta* was also a pest of cultivated sour cherries (*Prunus cerasus* L.) in New York, and similar records followed from other eastern localities. The first native hosts of *fausta* were not reported until 1918 when Severin found the pin, or fire cherry (*Prunus pennsylvanica* L. f.), to be infested exclusively with this species. Farleman (1932) also reared *fausta* from the fruits of *P. serotina* Ehrh., *P. virginiana* L., and *P. mahaleb* L., while Glasgow (1933) found *P. pennsylvanica* to be the preferred host of this species, although he was able to rear a few individuals from *P. virginiana* and *P. mahaleb*. Mackie (1940) recorded the western population of *fausta* infesting the fruits of *P. emarginata* (Dougl.) D. Dietr. With the possible exception of the isolated population of *P. emarginata* in Arizona, *fausta* probably infests the fruits of this plant over most of its range in western North America.

In the West, *fausta* does not effectively compete with *indifferens* when both occur in the same locality. Frick et al. (1954)



found that of 995 pupae sifted from soil under a *P. emarginata* tree, only four were *fausta*. The black cherry fruit fly in most areas emerges and is most active approximately one to three weeks before *cingulata*. The only known exception is the Vancouver Island population which emerges from two weeks to a month later than *cingulata* (Raine and Andison, 1958). In California, *fausta* is usually found at higher altitudes than *indifferens* (Wasbauer and Blanc, 1962, personal communication). This fact, along with the difference in emergence periods, may act to reduce competition between *fausta* and *indifferens*.

Distribution (Map 14). Neither eastern nor western populations of *R. fausta* extend as far north or south as their host plants. The eastern population, following the pattern common to many other *Rhagoletis* species, does not extend westward beyond the 100th meridian.

LITERATURE CITED

- AHRENDT, L. W. A. 1961. *Berberis* and *Mahonia*, a taxonomic revision. J. Linn. Soc. Bot., **57**: 1-410.
- ALDRICH, J. M. 1909. The fruit-infesting forms of the dipterous genus *Rhagoletis*, with one new species. Canad. Ent., **41**: 69-73.
- . 1910. A decennial confession. Canad. Ent., **42**: 99-100.
- ANDREWARTHA, H. G. and L. C. BIRCH. 1954. The distribution and abundance of animals. Univ. of Chicago Press. 782 pp.
- ANONYMOUS. 1962. Cooperative economic insect report (U.S. Dept. Agr.), **12**: 889.
- . 1963. *Ibid.*, **13**: 855.
- . 1964. *Ibid.*, **14**: 1188.
- AXELROD, D. I. 1958. Evolution of the Madro-Tertiary geoflora. Bot. Rev., **24**: 433-509.
- BABB, G. F. 1902. Note on *Rhagoletis suavis* Lw. with a description of the larva and puparium. Ent. News, **13**: 242.
- BALDUF, W. V. 1959. Obligatory and facultative insects in rose hips, their recognition and bionomics. Ill. Biol. Monogr., **26**: 1-194.
- BANKS, N. 1912. The structure of certain dipterous larvae with particular reference to those in human foods. U.S. Dept. Agr. Tech. Series, No. 22. 44 pp.
- BARNES, M. M. 1959. Radiotracer labeling of a natural tephritid population and flight range of the walnut husk fly. Ann. Amer. Ent. Soc., **52**: 90-92.
- BARNES, M. M. and H. T. OSBORN. 1958. Attractants for the walnut husk fly. J. Econ. Ent., **51**: 686-689.
- BENJAMIN, F. H. 1934. Descriptions of some native trypetid flies with notes on their habits. U.S. Dept. Agr. Tech. Bull., No. 401. 95 pp.
- BLANC, F. L. and H. H. KEIFER. 1955. The cherry fruit fly in North America. Morphological differentiation between the eastern and western subspecies of the cherry fruit fly, *Rhagoletis cingulata* (Loew). Calif. Dept. Agr. Bull., **44**: 77-88.
- BOYCE, A. M. 1929. The walnut husk fly, *Rhagoletis juglandis* Cresson. J. Econ. Ent., **22**: 861-866.
- . 1934. Bionomics of the walnut husk fly, *Rhagoletis completa*. Hilgardia, **8**: 363-579.
- BRITTON, W. E. 1906. Fifth report of the state entomologist of Connecticut. Conn. Agr. Expt. Sta. Ann. Rept. (1905), **29**: 189-262.
- BROOKS, F. E. 1921. Walnut husk-maggot. U.S. Dept. Agr. Bull., **992**: 1-8.
- BROWN, W. L., JR. 1953. Revisionary studies in the ant tribe Dacetini. Amer. Midl. Nat., **50**: 1-137.
- BROWN, W. L. JR. and E. O. WILSON. 1956. Character displacement. Syst. Zool., **5**: 49-64.
- BROWNE, L. B. 1957a. The effect of light on the mating behavior of the Queensland fruit fly *Strumeta tryoni* Frogg. Austral. J. Zool., **5**: 145-158.
- . 1957b. An investigation of the low frequency of mating of the Queensland fruit fly *Strumeta tryoni* Frogg. Austral. J. Zool., **5**: 159-163.
- BRUES, C. T. 1924. The specificity of food plants in the evolution of phytophagous insects. Amer. Nat., **58**: 127-144.
- BUSH, G. L. 1962. The cytotaxonomy of the larvae of some Mexican fruit flies in the genus *Anastrepha* (Tephritidae, Diptera). Psyche, **69**: 87-101.
- . 1965. The genus *Zonosemata* with notes on the cytology of two species. Psyche, **72**: 307-323.
- CAMP, W. H. 1941. Studies in the Ericales; A review of the North American Gaylussacae; with remarks on the origin and mi-

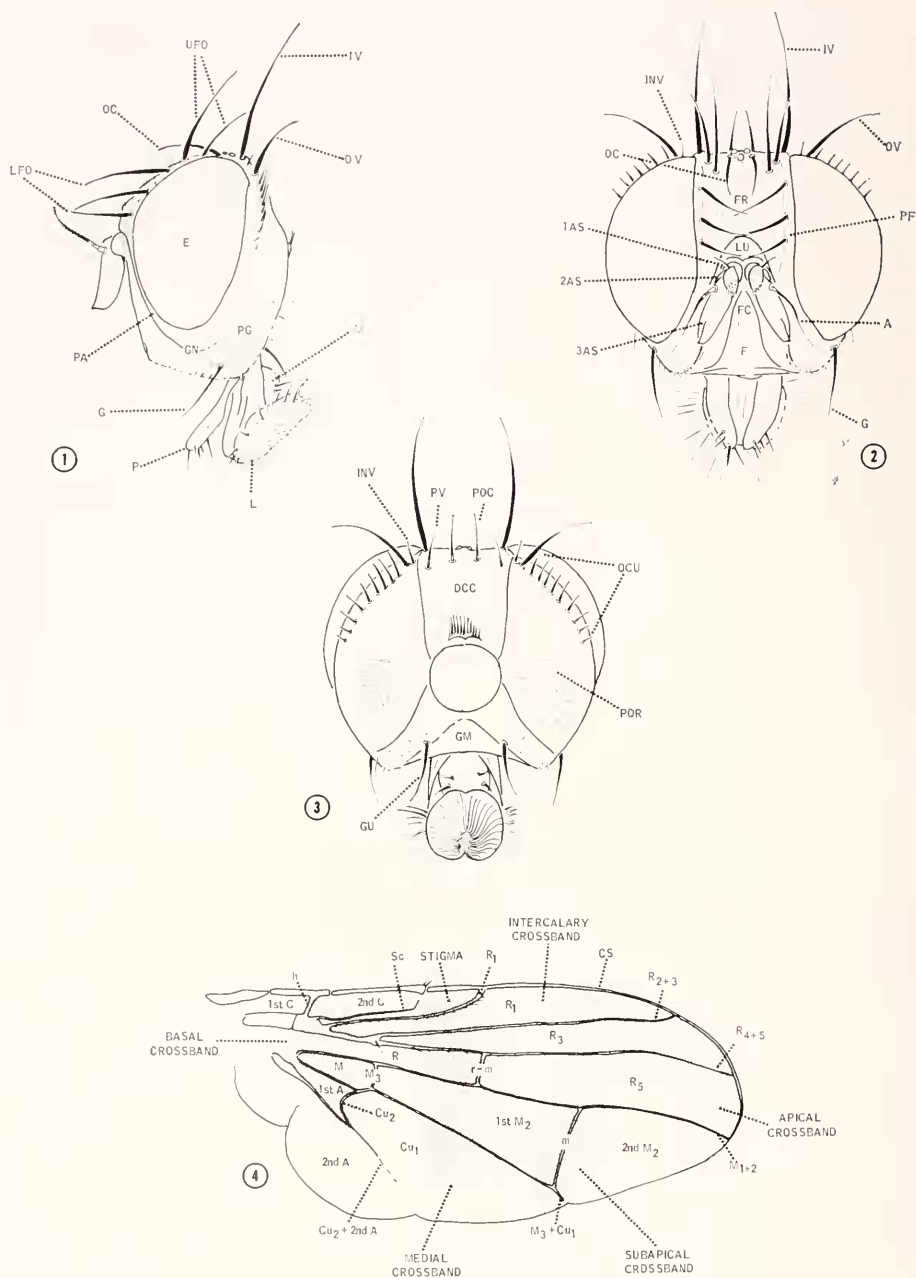
- gration of the group. *Bull. Torrey Club*, **68**: 531-551.
- . 1942. A survey of the American species of *Vaccinium*, subgenus *Eutaccinium*. *Brittonia*, **4**: 205-247.
- . 1945. The North American blueberries with notes on other groups of Vacciniaceae. *Brittonia*, **5**: 203-275.
- CHANEY, R. W. 1947. Tertiary centers and migration routes. *Ecol. Monogr.*, **17**: 139-148.
- CHRISTENSON, L. D. and R. H. FOOTE. 1960. Biology of fruit flies. *Ann. Rev. Ent.*, **5**: 171-192.
- COCKERELL, T. D. A. 1915. British fossil insects. *Proc. U.S. Nat. Mus.*, **49**: 469-499.
- . 1916. Some American fossil insects. *Proc. U.S. Nat. Mus.*, **51**: 89-106.
- . 1917. New Tertiary insects. *Proc. U.S. Nat. Mus.*, **52**: 373-384.
- . 1924. Fossil insects in the United States National Museum. *Proc. U.S. Nat. Mus.*, **64**: 1-15.
- . 1925. The Eocene fossil fly *Eophlebotomyia*. *Psyche*, **32**: 229-230.
- COLLIN, J. E. 1947. The British genera of Trypetidae (Diptera) with notes on a few species. *Ent. Rec. and J. Variation*, **59** (Suppl.): 1-14.
- CRESSON, E. T., JR. 1920. Descriptions of new North American acalyptrate Diptera II (Trypetidae, Sapromyzidae). *Ent. News*, **31**: 65-66.
- . 1929. A revision of the North American species of fruit-flies of the genus *Rhagoletis* (Diptera: Trypetidae). *Trans. Amer. Ent. Soc.*, **55**: 401-414.
- CURRAN, C. H. 1932. New North American Diptera with notes on others. *Amer. Mus. Nov.*, No. 526: 1-13.
- DEAN, R. W. 1933. Morphology of the digestive tract of the apple maggot fly, *Rhagoletis pomonella* Walsh. *New York State Coll. Agr. Tech. Bull.*, **215**: 1-17.
- . 1935. The anatomy and postpupal development of the female reproductive system in the apple maggot fly *Rhagoletis pomonella* Walsh. *New York State Agr. Expt. Sta. Tech. Bull.*, **229**: 1-31.
- DIRKS, C. O. 1935. Larval production and adult emergence of the apple fruit fly in relation to apple varieties. *J. Econ. Ent.*, **28**: 198-203.
- DOANE, R. W. 1898. A new trypetid of economic importance. *Ent. News*, **9**: 69-72.
- DRESSLER, R. L. 1954. Some floristic relationships between Mexico and the United States. *Rhodora*, **56**: 81-96.
- ELLERTSON, F. E. 1961. New host records for *Rhagoletis cingulata indifferens* in Oregon. *Pan-Pacific Ent.*, **37**: 116.
- FARLEMAN, M. G. 1932. Note on cherry fruit fly oviposition. *J. Econ. Ent.*, **25**: 1048.
- . 1933. Observations on the habits of flies belonging to the genus *Rhagoletis*. *J. Econ. Ent.*, **26**: 825-828.
- FÉRON, M. 1957. Le comportement de ponte de *Ceratitis capitata* Wied. Influence de la lumière. *Rev. Path. Vég. Ent. Agr. Fr.*, **36**: 127-143.
- . 1960. L'appel sonore du mâle dans le comportement sexuel de *Dacus oleae* Gmel. *Bull. Soc. Ent. Fr.*, **65**: 139-143.
- . 1962. Le comportement de reproduction chez la mouche Méditerranéenne des fruit *Ceratitis capitata* Wied. (Dipt. Trypetidae). Comportement sexuel—comportement de ponte. University of Paris Ph.D. thesis. Series A, No. 3868. No. d'ordre: 4719.
- FLINT, R. F. 1957. Glacial and Pleistocene geology. John Wiley and Sons, New York. 553 pp.
- FLORIN, R. 1963. The distribution of conifer and taxal genera in time and space. *Acta Horti Bergiani*, **20**: 121-312.
- FOOTE, R. H. 1960. A new tephritid genus, *Rhagoletoides*, with notes on its distribution and systematic position (Diptera, Tephritidae). *Ent. News*, **71**: 145-149.
- FOOTE, R. H. and F. L. BLANC. 1963. The fruit flies or Tephritidae of California. *Bull. Calif. Insect Surv.*, **7**: 1-117.
- FRICK, K. E., H. G. SIMKOVER, and H. S. TELFORD. 1954. Bionomics of the cherry fruit flies in eastern Washington. *Washington Agr. Expt. Sta. Tech. Bull.*, **13**: 1-66.
- GAHAN, A. B. 1930. Synonymical and descriptive notes on parasitic Hymenoptera. *Proc. U. S. Nat. Mus.*, **77**: 1-12.
- GARCÉS, O. C. and F. L. GALLEGOS. 1947. Algunas enfermedades y plagas que atacan al manzano en Antioquia. *Rev. Fac. Nac. Agron.*, **7**: 443-494.
- GLASGOW, H. 1933. The host relations of our cherry fruit flies. *J. Econ. Ent.*, **26**: 431-438.
- GREEN, P. S. 1958. A monographic revision of *Osmanthus* in Asia and America. *Notes Roy. Bot. Garden Edinburgh*, **22**: 439-542.
- GREENE, C. T. 1927. Larvae of *Rhagoletis*

- pomonella* Walsh. J. Washington Acad. Sci., **17**: 183.
- HÄFLIGER, E. 1953. Das Auswahlvermögen der Kirschenfliege bei der Eiablage (eine statistische Studie). Mitt. Schweiz. Ent. Gesell., **26**: 258–264. (Vide Rev. Appl. Ent., **44**: 175.)
- HALL, J. A. 1938. Further observations on the biology of the apple maggot (*Rhagoletis pomonella* Walsh). Rept. Ent. Soc. Ont., **69**: 53–58.
- . 1943. Notes on the dogwood fly, a race of *Rhagoletis pomonella* (Walsh). Canad. Ent., **75**: 202.
- HENDEL, F. 1927. Trypetidae. In Lindner, E. (ed.), Die Fliegen der palaearktischen Region, **5**: 1–221.
- HERING, E. M. 1958. Zwei neue paläarktische *Rhagoletis* (Dipt., Trypet.). Stuttgarter Beit. Naturk., **7**: 1–4.
- HERRICK, G. W. 1920. The apple maggot in New York. Cornell Univ. Agr. Expt. Sta. Bull., **402**: 89–101.
- HOWDEN, H. 1963. Speculations on some beetles, barriers and climates during the Pleistocene and pre-Pleistocene periods in some non-glaciated portions of North America. Syst. Zool., **12**: 178–201.
- ILLINGWORTH, J. F. 1912. A study of the biology of the apple maggot (*Rhagoletis pomonella*), together with an investigation of methods of control. Cornell Univ. Agr. Expt. Sta. Bull., **324**: 129–187.
- JONES, G. N. 1940. A monograph of the genus *Symphoricarpos*. J. Arnold Arb., **21**: 201–252.
- KEIFER, H. H. 1938. Systematic entomology. Calif. Dept. Agr. Bull., **27**: 662.
- LATHROP, F. H. AND L. C. MCALISTER, JR. 1931. The blueberry maggot and its control in eastern Maine. U.S. Dept. Agr. Circ., No. 196. 13 pp.
- LATHROP, F. H. AND R. C. NEWTON. 1933. The biology of *Opinus melleus* Gahan, a parasite of the blueberry maggot. J. Agr. Res., **46**: 143–160.
- LATHROP, F. H. AND C. B. NICKELS. 1931. The blueberry maggot from an ecological viewpoint. Ann. Amer. Ent. Soc., **24**: 260–274.
- . 1932. The biology and control of the blueberry maggot in Washington County, Maine. U.S. Dept. Agr. Tech. Bull., No. 275. 76 pp.
- LAWRENCE, G. H. M. 1951. Taxonomy of vascular plants. Macmillan, New York. 823 pp.
- LEWIS, W. H. 1959. A monograph of the genus *Rosa* in North America. I. *R. acicularis*. Brittonia, **11**: 1–24.
- LLOYD, J. J. 1963. Tectonic history of the south Central-American orogen. In Backbone of the Americas, pp. 88–100. Publ. Amer. Assoc. Petroleum Geologists.
- LOEW, H. 1862. Die europaischen Bohrfliegen (Trypetidae). Vienna. 128 pp.
- . 1864. On the Diptera or two-winged insects of the amber-fauna. (Ueber die Diptern-fauna des Bernsteins). Amer. J. Sci., (2) **37**: 305–324.
- MACGINTIE, H. D. 1958. Climate since the late Cretaceous. In Huxley, C. L. (ed.), Zoogeography, pp. 61–79. AAAS Publ. 51, Washington, D.C.
- MACKIE, D. B. 1940. Cherry fruit flies in California (a preliminary note). Calif. Dept. Agr. Bull., **29**: 157.
- MAERZ, A. AND M. R. PAUL. 1950. A dictionary of color. 2nd ed. McGraw-Hill, New York. 208 pp.
- MANNING, W. E. 1957. The genus *Juglans* in Mexico and Central America. J. Arnold Arb., **38**: 121–150.
- MARCOVITCH, S. 1915. The biology of the juniper berry insects, with descriptions of new species. Ann. Amer. Ent. Soc., **8**: 163–181.
- MARTIN, P. S. AND B. E. HARRELL. 1957. The Pleistocene history of temperate biotas in Mexico and eastern United States. Ecology, **38**: 468–480.
- MAYR, E. 1963. Animal species and evolution. Belknap Press, Harvard Univ., Cambridge, Mass. 797 pp.
- MCALISTER, L. C. 1932. An observation of a maggot, *Rhagoletis pomonella* Walsh, passing from one blueberry into an adjacent blueberry. J. Econ. Ent., **25**: 412–413.
- MCALISTER, L. C. AND W. H. ANDERSON. 1935. Insectary studies on the longevity and preoviposition period of the blueberry maggot and on cross breeding with the apple maggot. J. Econ. Ent., **28**: 675–678.
- MCCRONE, J. D. 1963. Taxonomic status and evolutionary history of the *Geolycosa pikei* complex in the southeastern United States (Araneae, Lycosidae). Amer. Midl. Nat., **70**: 47–73.
- MCVAUGH, R. 1943. The status of certain anomalous native crabapples in eastern United States. Bull. Torrey Club, **70**: 418–429.
- . 1952. Suggested phylogeny of *Prunus*

- scrotina* and other wide-ranging phylads in North America. *Brittonia*, **7**: 317-346.
- MELANDER, A. L. 1949. A report on some Miocene Diptera from Florissant, Colorado. *Amer. Mus. Nov.*, No. 1407: 1-63.
- MIDDLEKAUFF, W. W. 1941. Some biological observations of the adults of the apple maggot and the cherry fruitflies. *J. Econ. Ent.*, **34**: 621-624.
- MONRO, J. 1953. Stridulation in the Queensland fruit-fly (*Dacus (Strumeta) tryoni* Frogg.). *Austral. J. Sci.*, **16**: 60-62.
- MUESEBECK, C. F. W. 1956. On *Opius ferrugineus* Gahan and two closely similar new species. (Hymenoptera: Braconidae). *Ent. News*, **67**: 99-102.
- MUNRO, H. K. 1947. African Trypetidae (Diptera). *Mem. Ent. Soc. South Africa*, **1**: 1-284.
- NICHOLSON, D. J. 1929-30. Report upon native Trypetidae of Florida. U.S. Dept. Agr., Bur. Ent. (unpubl. rept.)
- O'KANE, W. C. 1914. The apple maggot. New Hampshire Expt. Sta. Bull., No. 171. 120 pp.
- PHILLIPS, V. T. 1923. A revision of the Trypetidae of northeastern America. *J. New York Ent. Soc.*, **31**: 119-155.
- . 1946. The biology and identification of trypetid larvae (Diptera: Trypetidae). *Mem. Amer. Ent. Soc.*, **12**: 1-161.
- PICKETT, A. D. 1937. Studies on the genus *Rhagoletis* (Trypetidae) with special reference to *Rhagoletis pomonella* (Walsh). *Canad. J. Res.*, (D) **15**: 53-75.
- PICKETT, A. D. AND M. E. NEARY. 1940. Further studies on *Rhagoletis pomonella* (Walsh). *Scient. Agr.*, **20**: 551-556.
- PIPER, C. V. AND R. W. DOANE. 1898. Insects injurious to currants and gooseberries. Washington Agr. Expt. Sta. Bull., No. 36. 16 pp.
- PLANK, H. K. 1923. Scientific note on *Rhagoletis tabellaria* (Fitch). *J. Econ. Ent.*, **16**: 99.
- PORTER, B. A. 1928. The apple maggot. U.S. Dept. Agr. Tech. Bull., No. 66. 48 pp.
- PORTER, B. A. AND C. H. ALDEN. 1921. *Ana-phoidea conotracheli* Girault (Hym.), an egg parasite of the apple maggot. *Proc. Ent. Soc. Washington*, **23**: 62-63.
- RAINE, J. AND H. ANDISON. 1958. Life histories and control of cherry fruit flies on Vancouver Island, British Columbia. *J. Econ. Ent.*, **51**: 592-595.
- RICHARDS, P. W. 1952. The tropical rain forest. Cambridge Univ. Press. 450 pp.
- RICKETT, H. W. 1944. *Cornus stolonifera* and *Cornus occidentalis*. *Brittonia*, **5**: 149-159.
- . 1945. Cornales. *N. Amer. Flora*, **28** B: 297-316.
- . 1950. *Cornus* in Mexico, with notes on the evolution of the genus. *Anal. Inst. Biol. (Mex.)*, **21**: 83-94.
- ROHDENDORF, B. B. 1961. Paläarktische Arten der Gattung *Rhagoletis* Loew (Diptera, Trypetidae) und verwandte Bohrfliegengattungen. *Ent. Obozr.*, **40**: 176-201.
- ROSS, W. A. 1913. Recent work on the apple maggot in Ontario. *Rept. Ent. Soc. Ont.*, **43**: 67-71.
- SAX, K. 1931. The origin and relationships of the Pomoideae. *J. Arnold Arb.*, **12**: 3-22.
- . 1933. The origin of the Pomoideae. *Proc. Amer. Soc. Hort. Sci.*, **30**: 147-150.
- SEVERIN, H. H. R. 1918. A native food plant of *Rhagoletis fausta* O.S. *J. Econ. Ent.*, **11**: 325-327.
- SHARP, A. J. 1953. Notes on the flora of Mexico: world distribution of the woody dicotyledonous families and the origin of the modern vegetation. *J. Ecol.*, **41**: 374-380.
- SILVESTRI, F. 1916. Sulle specie di Trypaneidae (Diptera) del genere *Carponymia* dannose ai frutti di *Zizyphus*. *Boll. Lab. Zool. Portici*, **11**: 170-182.
- SMITH, H. S. 1941. Racial segregation in insect populations and its significance in applied entomology. *J. Econ. Ent.*, **34**: 1-12.
- SMYTH, E. G. 1960. A new tephritid fly injurious to tomatoes in Peru. *Calif. Dept. Agr. Bull.*, **49**: 16-22.
- SPIETH, H. T. 1952. Mating behavior within the genus *Drosophila* (Diptera). *Bull. Amer. Mus. Nat. Hist.*, **99**: 399-474.
- STANDLEY, P. C. 1922. Trees and shrubs of Mexico. Part 2. *Contrib. U.S. Nat. Herb.*, **23**: 171-515.
- STANDLEY, P. C. AND J. A. STEYERMARK. 1946. Flora of Guatemala. Part 4. *Fieldiana: Botany*, **24**: 489 pp.
- STEBBINS, G. L., JR. 1950. Variation and evolution in plants. Columbia Univ. Press, New York. 643 pp.
- STEYSKAL, G. C. 1957. The postabdomen of male acalyptrate Diptera. *Ann. Amer. Ent. Soc.*, **50**: 66-73.
- . 1961. The genera of Platystomatidae and Otitidae known to occur in America north of Mexico (Diptera, Acalyptratae). *Ann. Amer. Ent. Soc.*, **54**: 401-410.

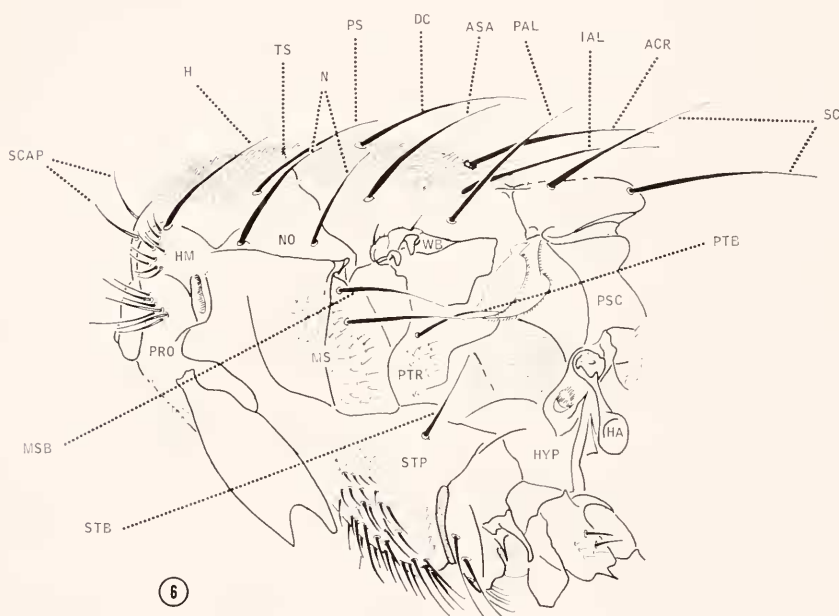
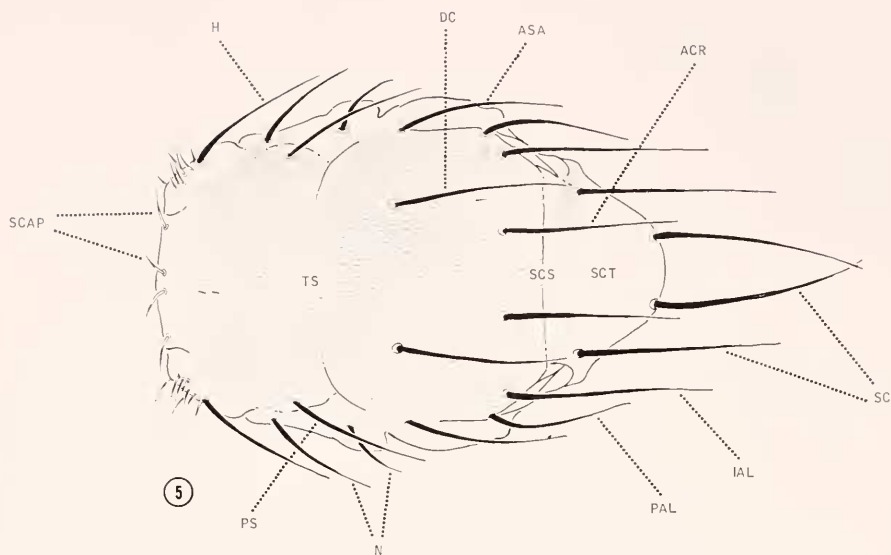
- STIRRETT, G. M. 1936. The walnut husk fly, *Rhagoletis suavis* Loew, in Ontario. Rept. Ent. Soc. Ont., **66**: 69.
- STONE, A. 1951. The *Rhagoletis* of roses (Dipt., Tephritidae). Proc. Ent. Soc. Washington, **53**: 45-48.
- THORPE, W. H. 1930. Biological races in insects and allied groups. Biol. Rev., **5**: 177-212.
- THORSTEINSON, A. J. 1960. Host selection in phytophagous insects. Ann. Rev. Ent., **5**: 193-218.
- TOMINIĆ, A. 1954. Ispitivanja muhe trešnjarice u Dalmaciji [Investigations on the cherry fruit-fly in Dalmatia]. Plant Prot., **23**: 44-62. (With English summary.)
- WALSH, B. D. 1867. The apple worm and the apple maggot. Amer. J. Hort., **2**: 338-343.
- WEBER, J. G. C. 1963. Study in the genus *Chaenomeles*, Rosaceae. Unpubl. Ph.D. thesis. Harvard Univ. 216 pp.
- WELLHOUSE, W. H. 1920. Wild hawthorns as hosts of apple, pear and quince pests. J. Econ. Ent., **13**: 388-391.
- . 1922. The insect fauna of the genus *Crataegus*: Trypetidae. New York (Cornell) Agr. Expt. Sta. Mem., **56**: 1085-1086.
- WHITE, M. J. D. 1957. Cytogenetics and systematic entomology. Ann. Rev. Ent., **2**: 71-90.
- WIESMANN, R. 1937. Das Wirtspflanzenproblem der Kirschfliege, *Rhagoletis cerasi* L. Landw. Jb. Schweiz, **51**: 1031-1044.
- WILSON, H. F. AND A. L. LOVETT. 1913. Miscellaneous insect pests of orchard and garden. Oregon Agr. Expt. Sta. Biennial Crop Pest and Hort. Rept., (1911-1912): 160.
- WILSON, K. A. AND C. E. WOOD, JR. 1959. The genera of Oleaceae in the southeastern United States. J. Arnold Arb., **40**: 369-384.
- WOOD, C. E., JR. 1961. The genera of Ericaceae in the southeastern United States. J. Arnold Arb., **42**: 10-80.
- WOODS, W. C. 1915a. Blueberry insects in Maine. Maine Agr. Expt. Sta. Bull., **244**: 249-288.
- . 1915b. *Biosteres rhagoletis* Richmond sp. n., a parasite of *Rhagoletis pomonella* Walsh. Canad. Ent., **47**: 293-295.
- ZIMMERMAN, E. C. 1960. Possible evidence of rapid evolution in Hawaiian moths. Evolution, **14**: 137-138.

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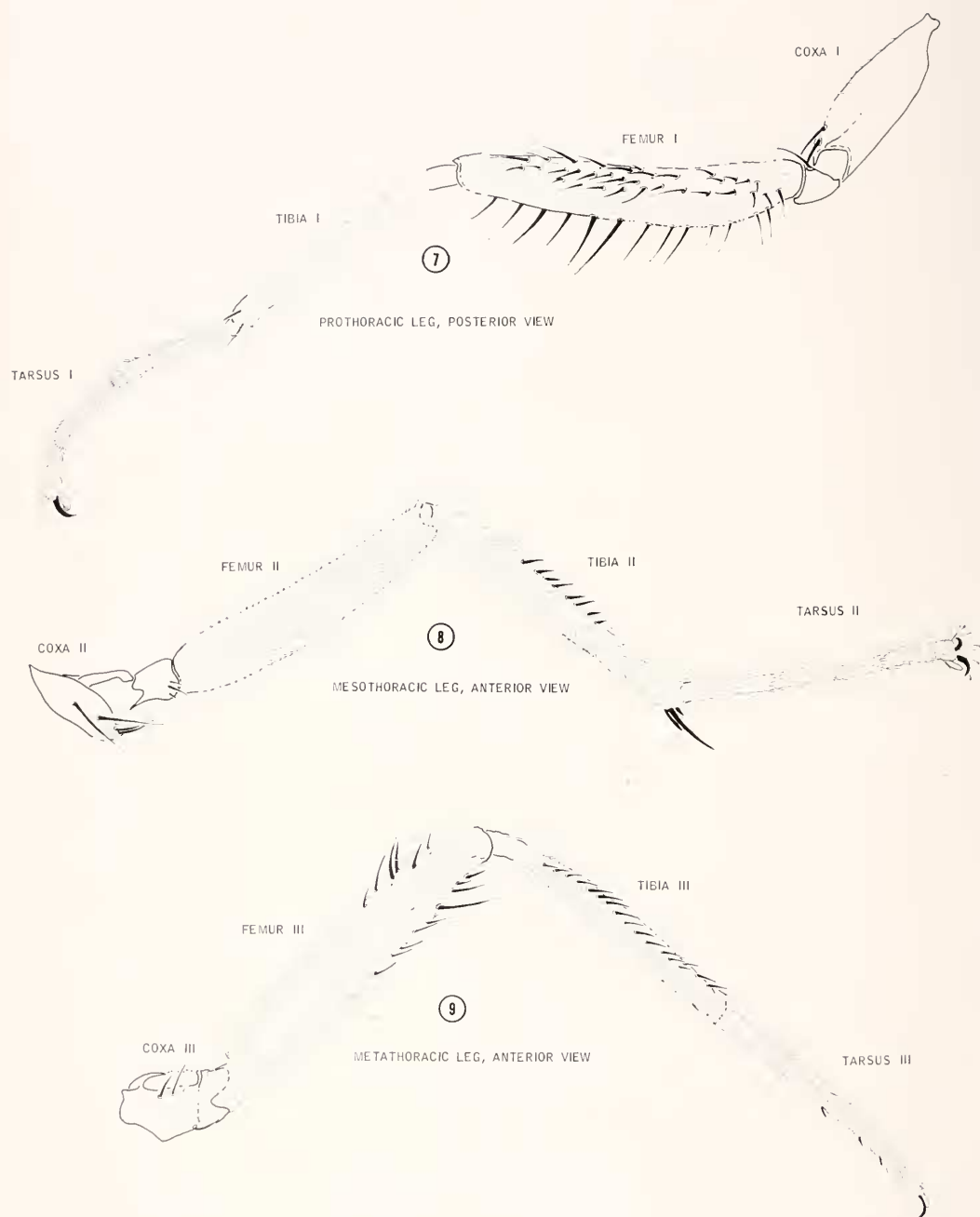


Figures 1-3. Chaetotaxy and areas of the head. Fig. 1, side view. Fig. 2, front view. Fig. 3, posterior view. Abbreviations: A, arista; E, eye; F, face; FC, facial carina; FR, frontalia; G, genal bristle; GM, gulamentum; GN, gena; GU, gular bristle; INV, intravertic bristle; IV, innervertic bristle; L, labella; LFO, lower fronto-orbital bristles; LU, lunule; M, mentum; OC, acellar bristle; OCC, occiput; OCU, postocellar bristles; OV, outervertic bristle; P, palpi; PA, parafacial; PF, parafrontal; PG, postgenae; POC, postocellar bristle; POR, postorbital region; PV, postvertical bristle; UFO, upper fronto-orbital bristles; 1AS, first antennal segment; 2AS, second antennal segment; 3AS, third antennal segment.

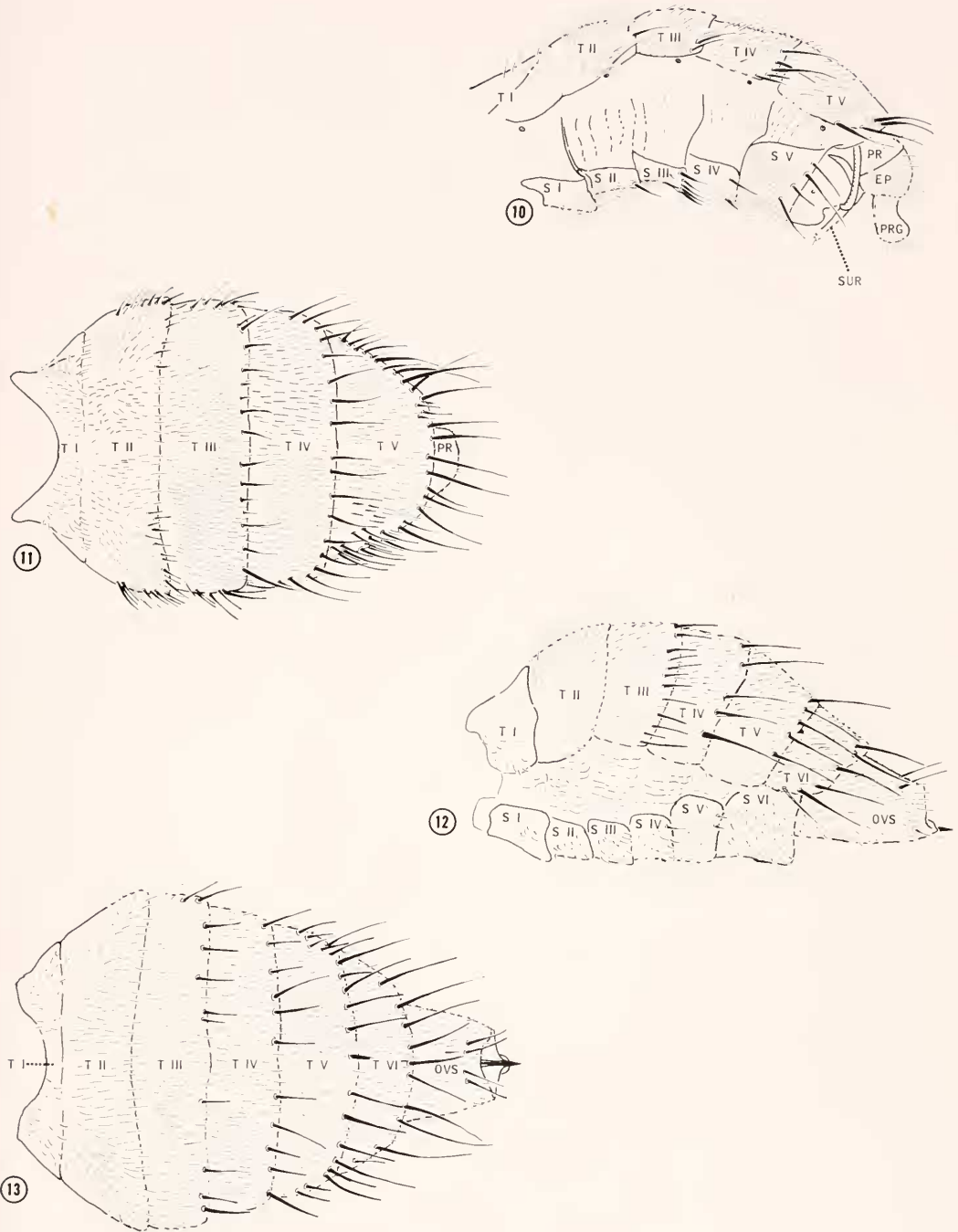
Figure 4. Wing showing cells, venation, and generalized wing pattern.



Figures 5-6. Chaetotaxy and areas of the thorax. Fig. 5, dorsal view. Fig. 6, side view. Abbreviations: ACR, acrostichal bristle; ASA, anterior supraalar; DC, dorsocentral bristle; H, humeral bristle; HA, haltere; HM, humerus; HYP, hypopleuron; IAL, intraalar bristle; MS, mesopleuron; MSB, mesopleural bristle; N, notopleural bristle; NO, notopleuron; PAL, postalar bristle; PRO, propleuron; PS, presutural bristle; PSC, postscutellum; PTB, pteropleural bristle; PTR, pteropleuron; SC, scutellar bristle; SCAP, scapular bristle; SCS, scutoscuteellar suture; SCT, scutellum; STB, sternopleural bristle; STP, sternopleuron; TS, transverse suture; WB, wing base.



Figures 7-9. Legs showing arrangement of major bristles. Fig. 7. Prothoracic leg, posterior view. Fig. 8. Mesothoracic leg, anterior view. Fig. 9. Metathoracic leg, anterior view.



Figures 10-13. Abdomen showing segmentation and position of bristles. Fig. 10, ♂, lateral view. Fig. 11, ♂, dorsal view. Fig. 12, ♀, lateral view. Fig. 13, ♀, dorsal view. Abbreviations: EP, epandrium; OVS, ovipositor sheath; PR, prandrium; PRG, prandiger; SUR, surstyli; T, tergites; S, sternites.

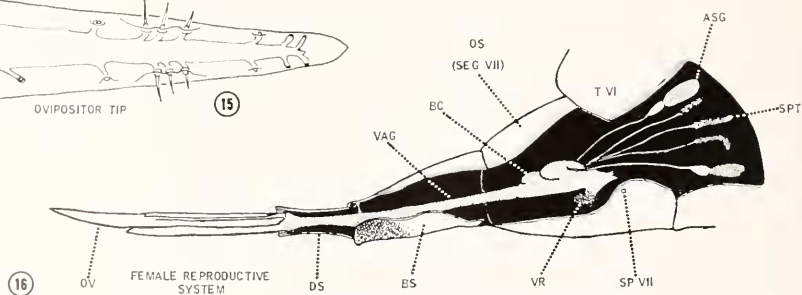
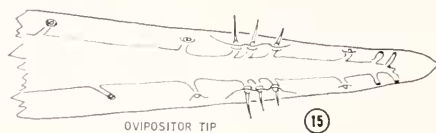
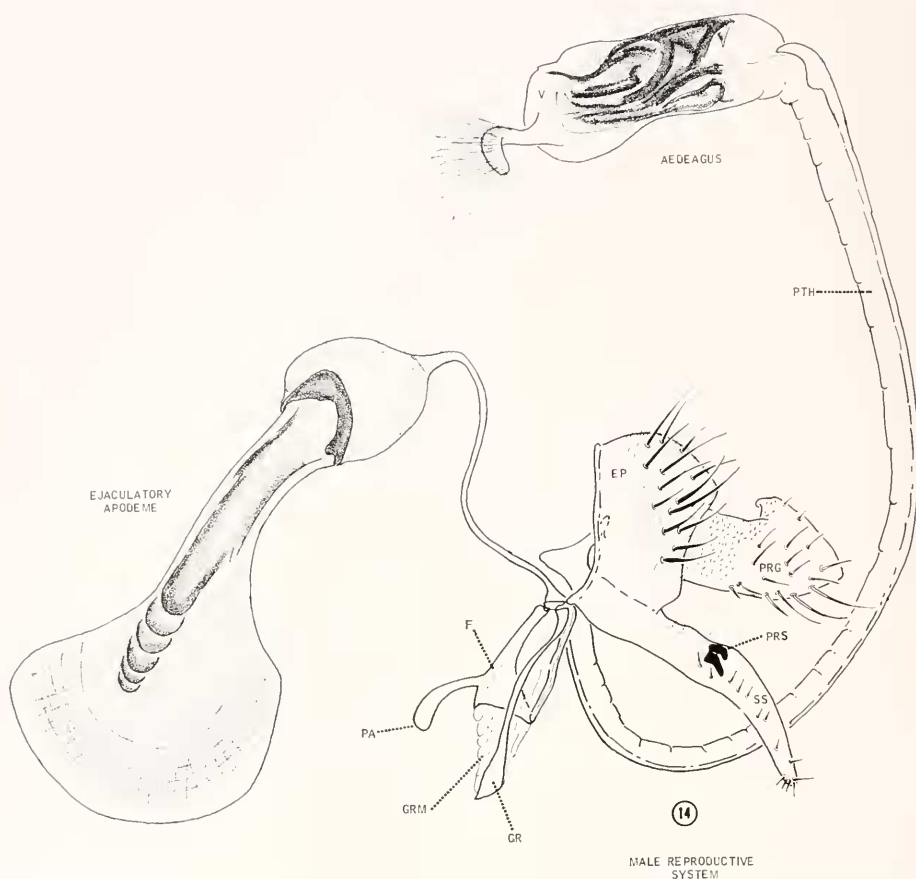
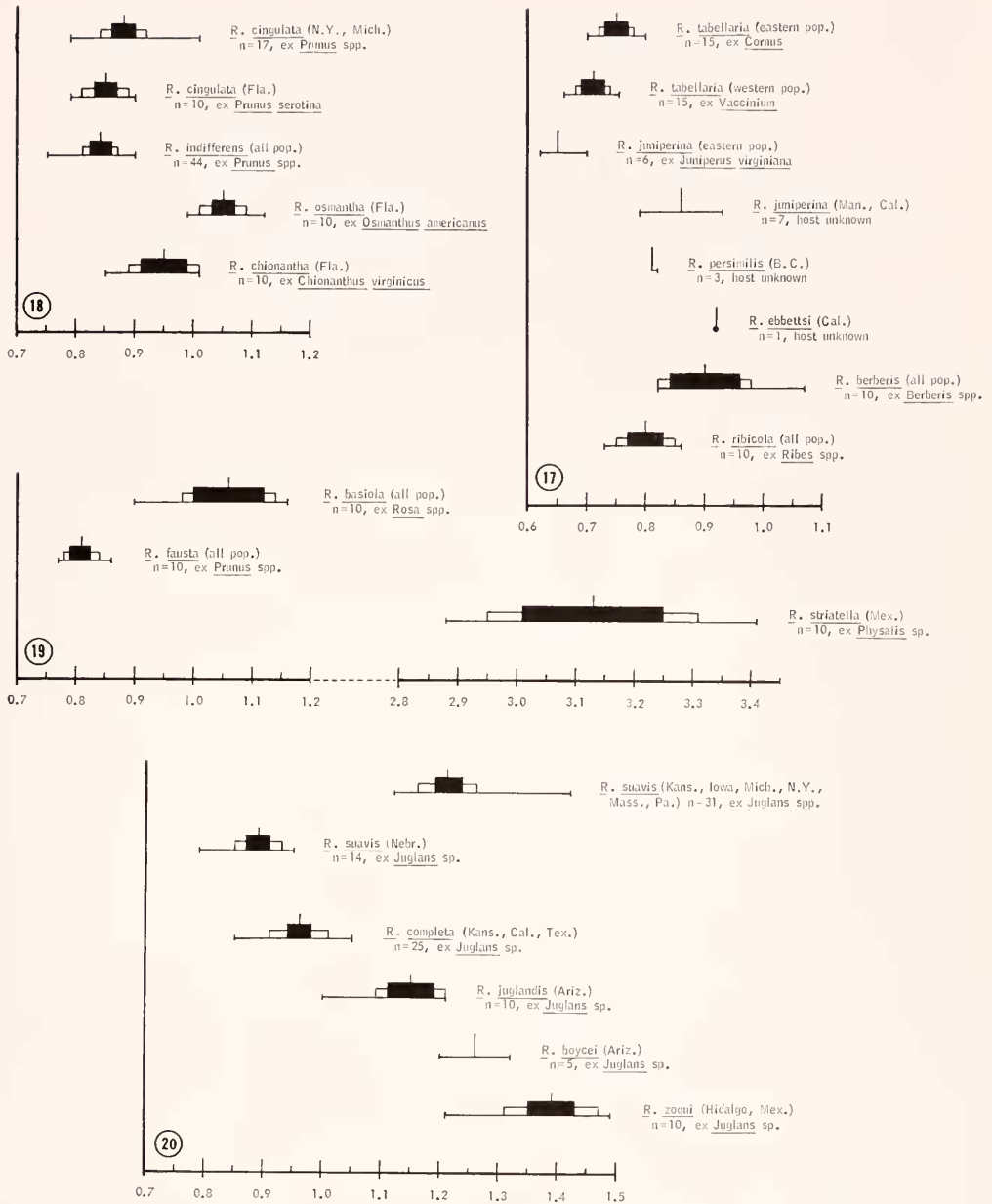


Figure 14. Terminalia of mole; EP, epandrium; F, fultella; GR, genital ring; GRM, genital ring membrane; PA, phallic apodeme; PRG, practiger; PRS, prenisetae; PTH, phallosome.

Figure 15. Detail of ovipositor tip showing three pairs of preopical setae.

Figure 16. Sclerotized portion of female reproductive system: ASG, accessory gland; BC, bursa copulatrix; BS, basal sheath; DS, distal sheath; OS, ovipositor sheath; OV, ovipositor; SEG, segment; SP, spiracle; SPT, spermatheca; T, tergite; VAG, vagina; VR, ventral receptacle.



Figures 17-20. Dice-Leraas diagrams showing interspecific variation in ovipositor length. Horizontal lines represent observed ranges, rectangular mark standard deviation, and solid black indicates 95 per cent confidence intervals for the mean. Fig. 17. *tabellaria* species group. Fig. 18. *cingulata* species group. Fig. 19. Miscellaneous species. Fig. 20. *suavis* species group.

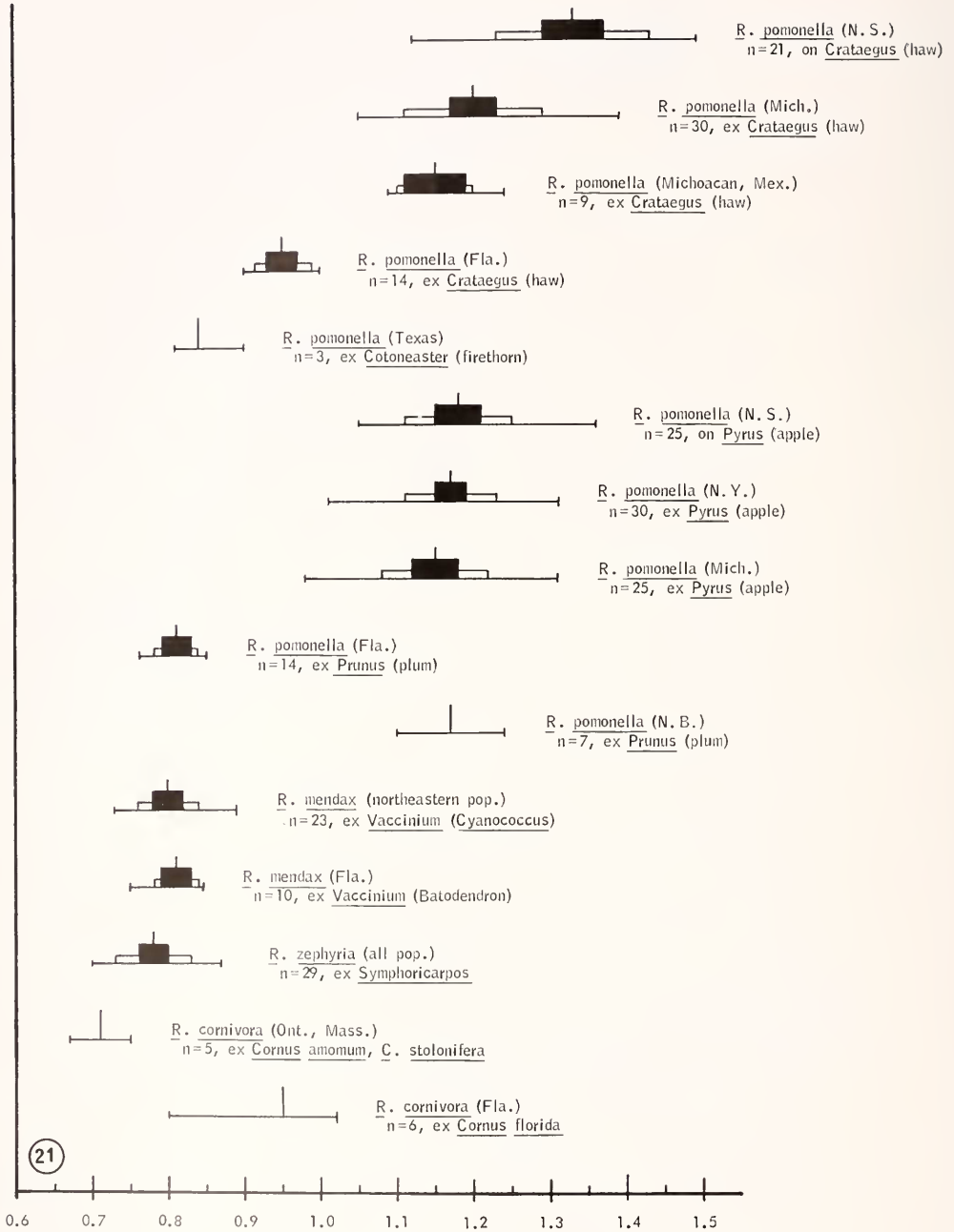
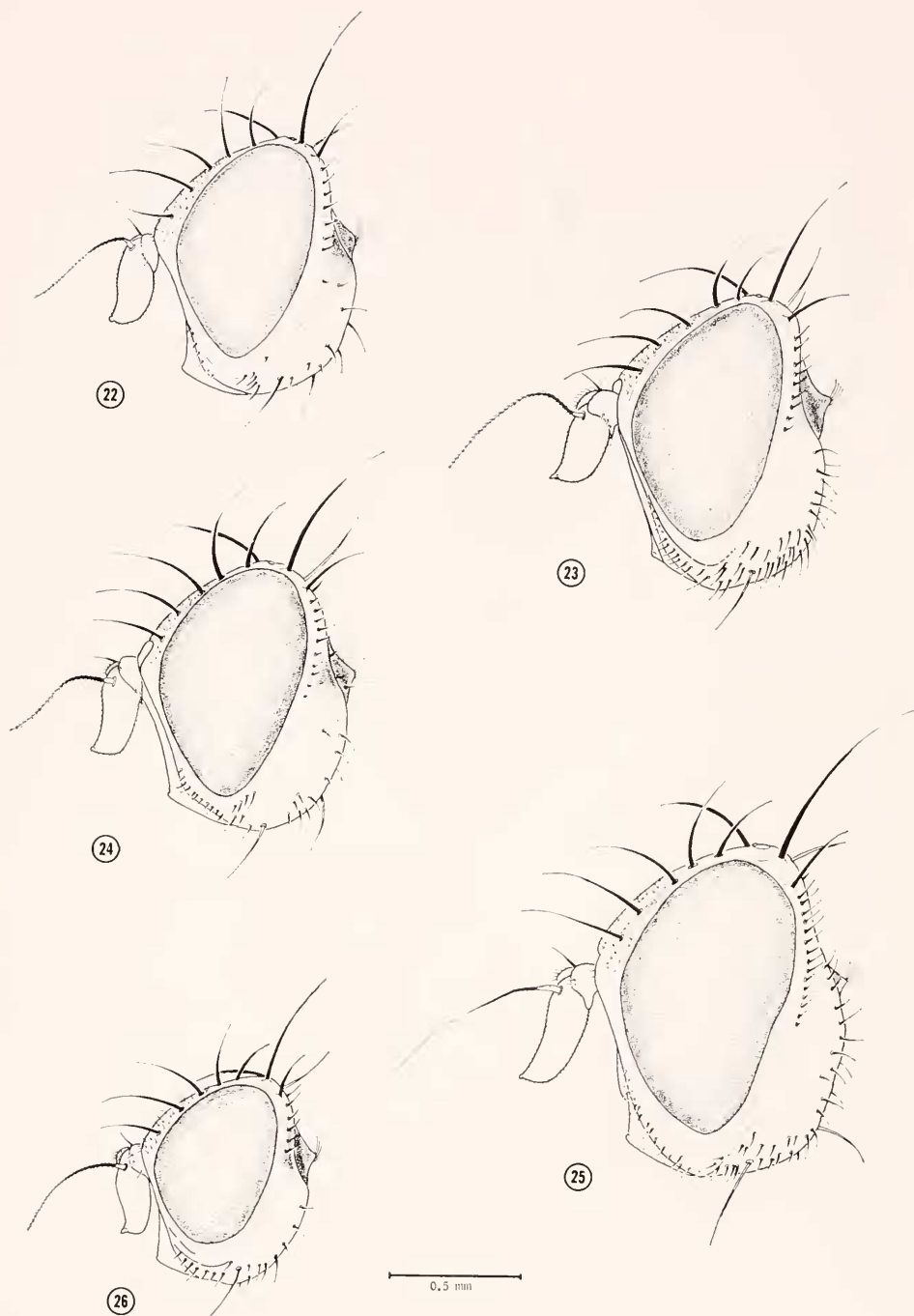
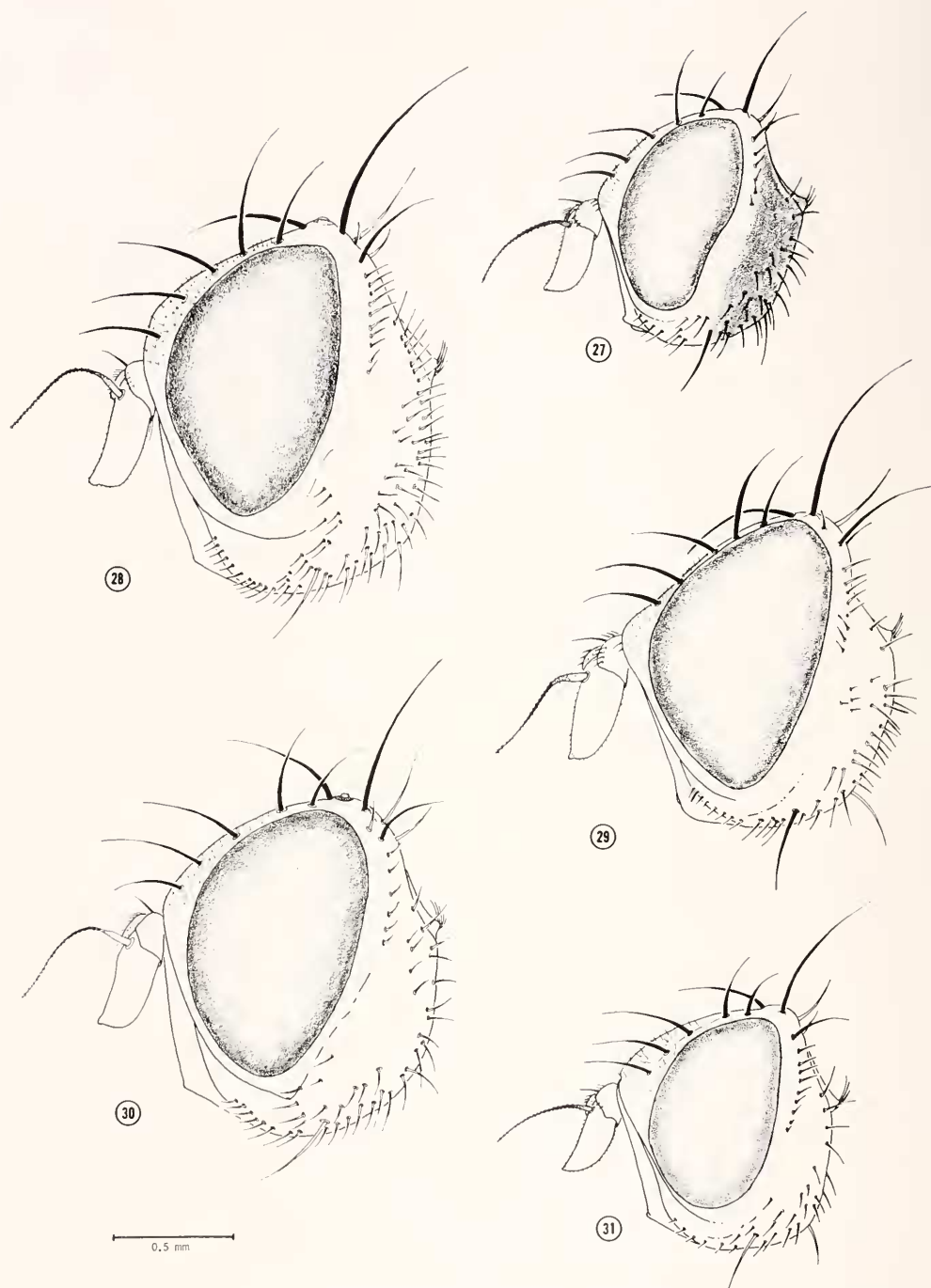


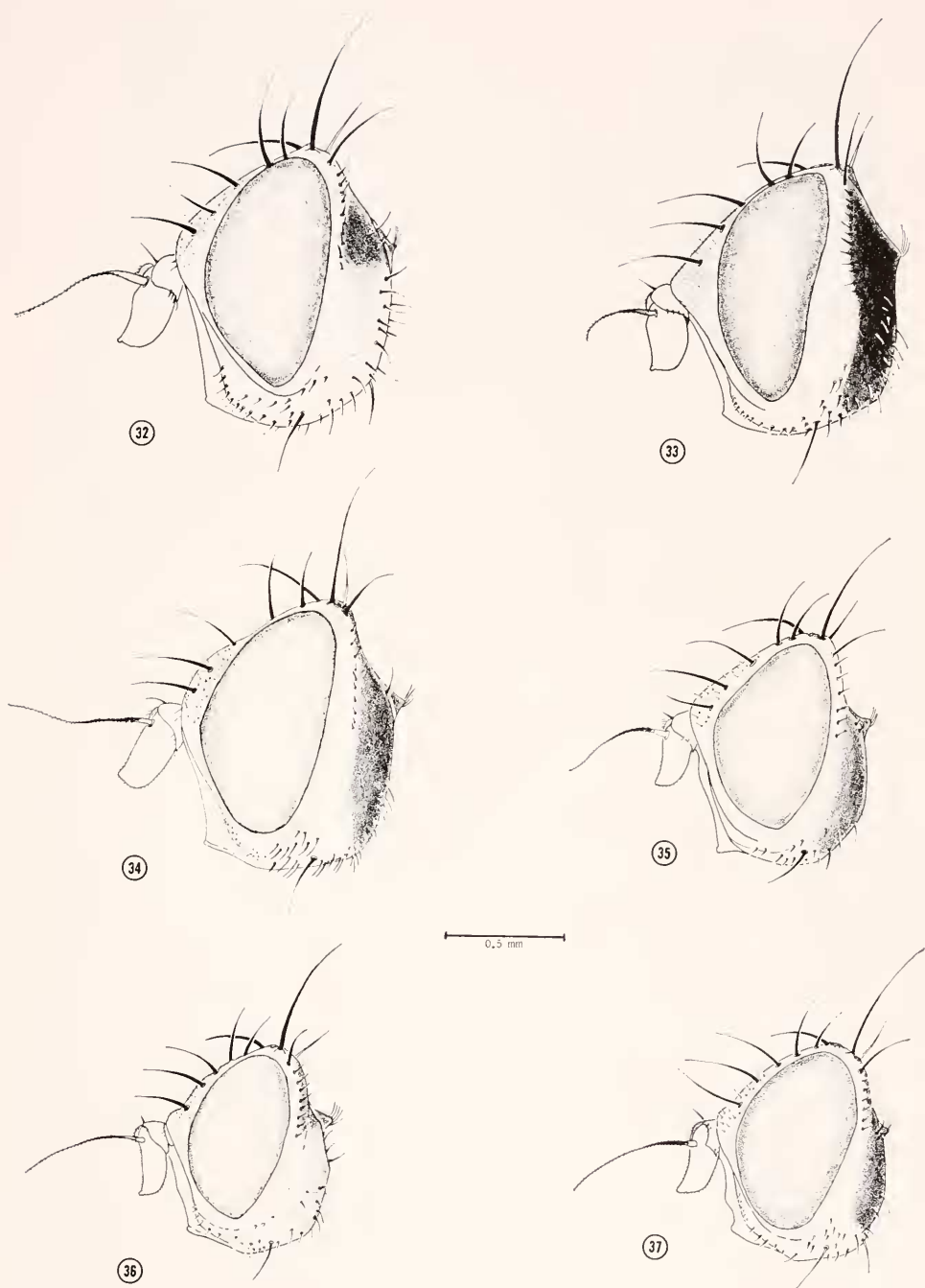
Figure 21. Dice-Leraas diagram showing interspecific variation in ovipositor length in species of the *pomonella* species group. Horizontal lines represent observed ranges, rectangular mark standard deviation, and solid black indicates 95 per cent confidence intervals for the mean.



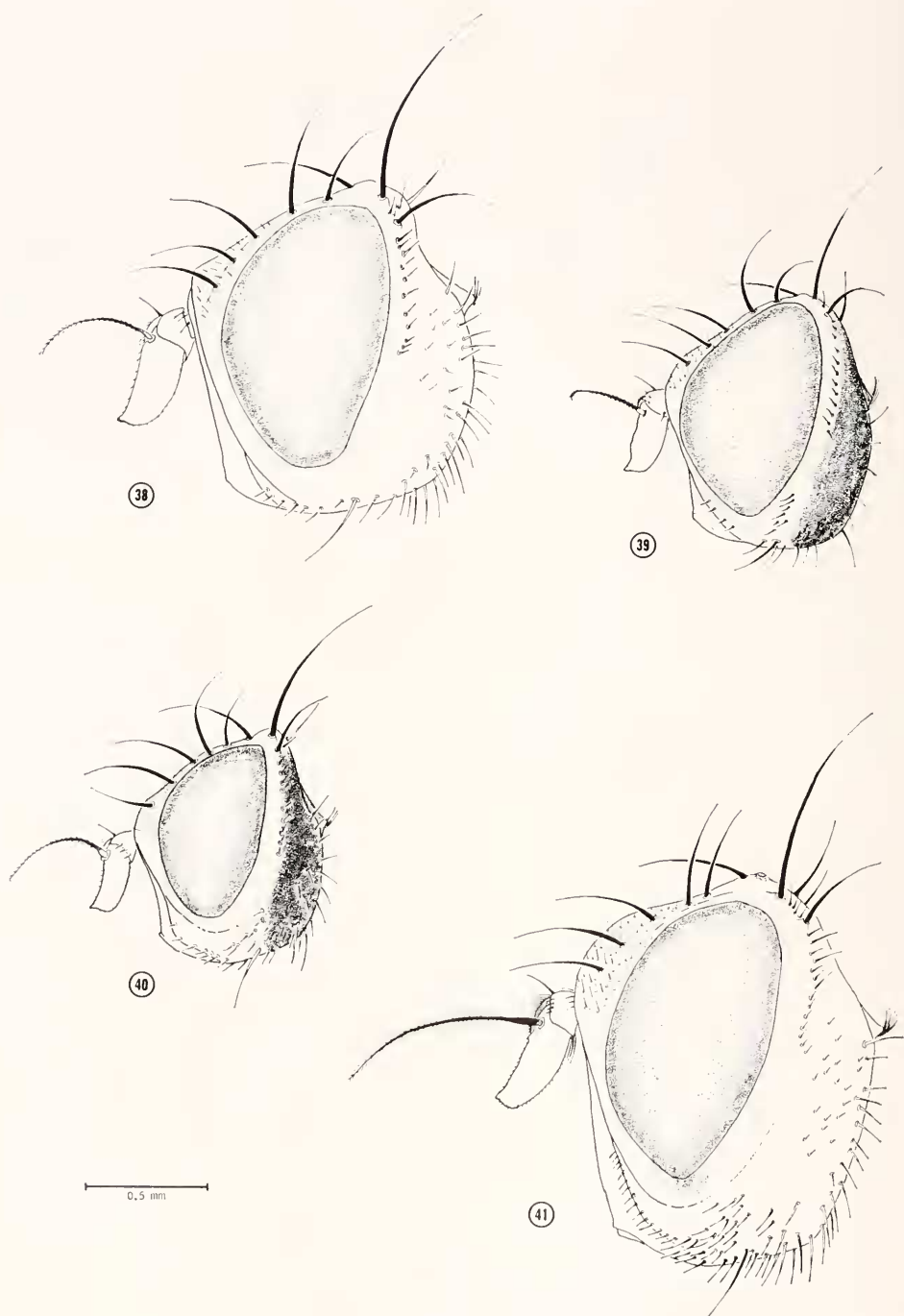
Figures 22–26. Lateral view of head of *Rhagoletis* species. Fig. 22. *R. zephyria* Snow, ♂, Calif. Fig. 23. *R. cornivora* n. sp., ♂, Mass. Fig. 24. *R. mendax* Curran, ♂, Maine. Fig. 25. *R. pamanella* (Walsh), ♂, Mass. Fig. 26. *R. mendax* Curran, ♂, Fla.



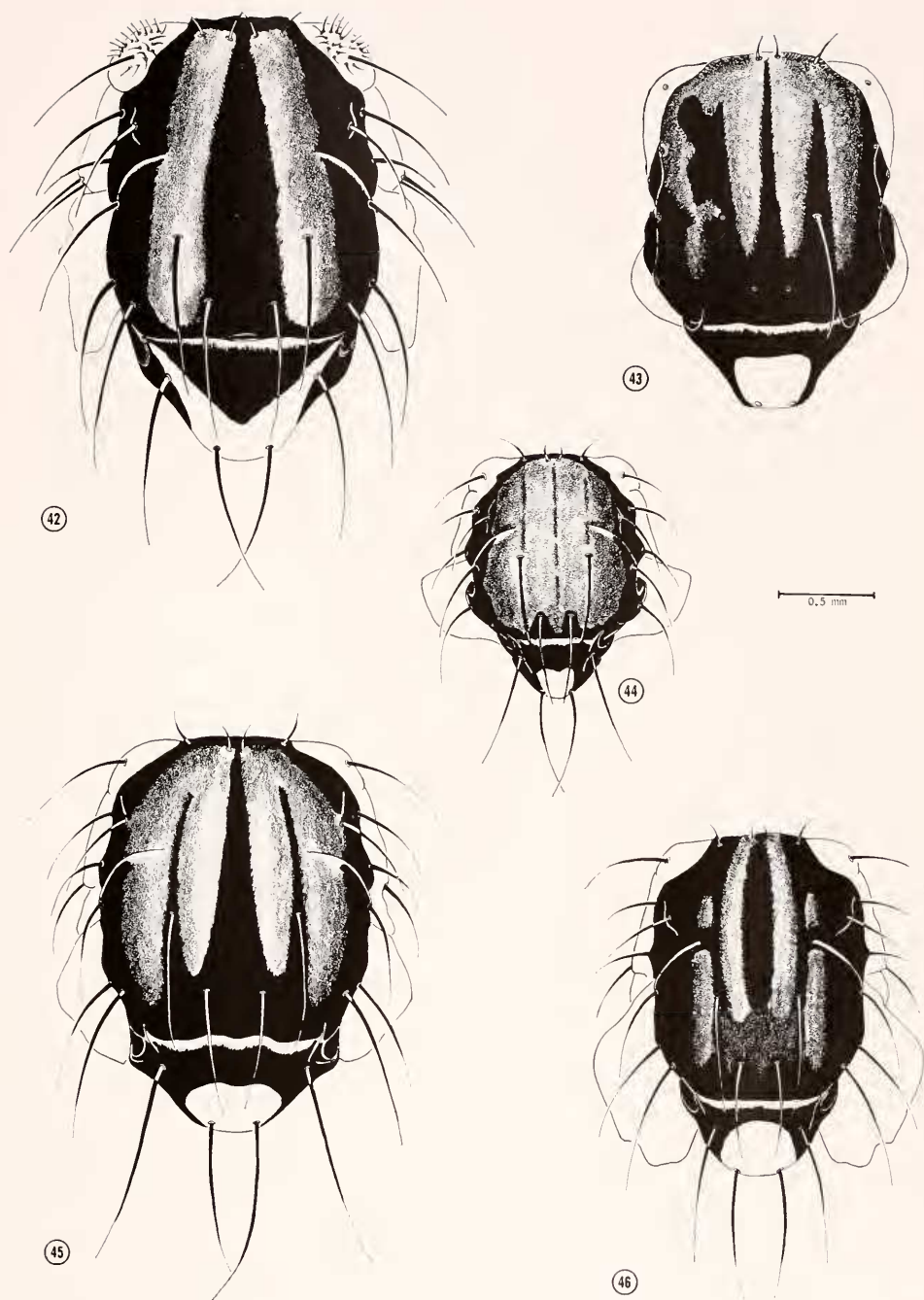
Figures 27-31. Lateral view of head of *Rhagoletis* species. Fig. 27. *R. boycei* Cresson, ♂, Ariz. Fig. 28. *R. completa* Cresson, ♂, Calif. Fig. 29. *R. zoqui* n. sp., ♂, Hidalgo, Mex. Fig. 30. *R. suavis* (Loew), ♂, Mass. Fig. 31. *R. juglandis* Cresson, ♂, Ariz.



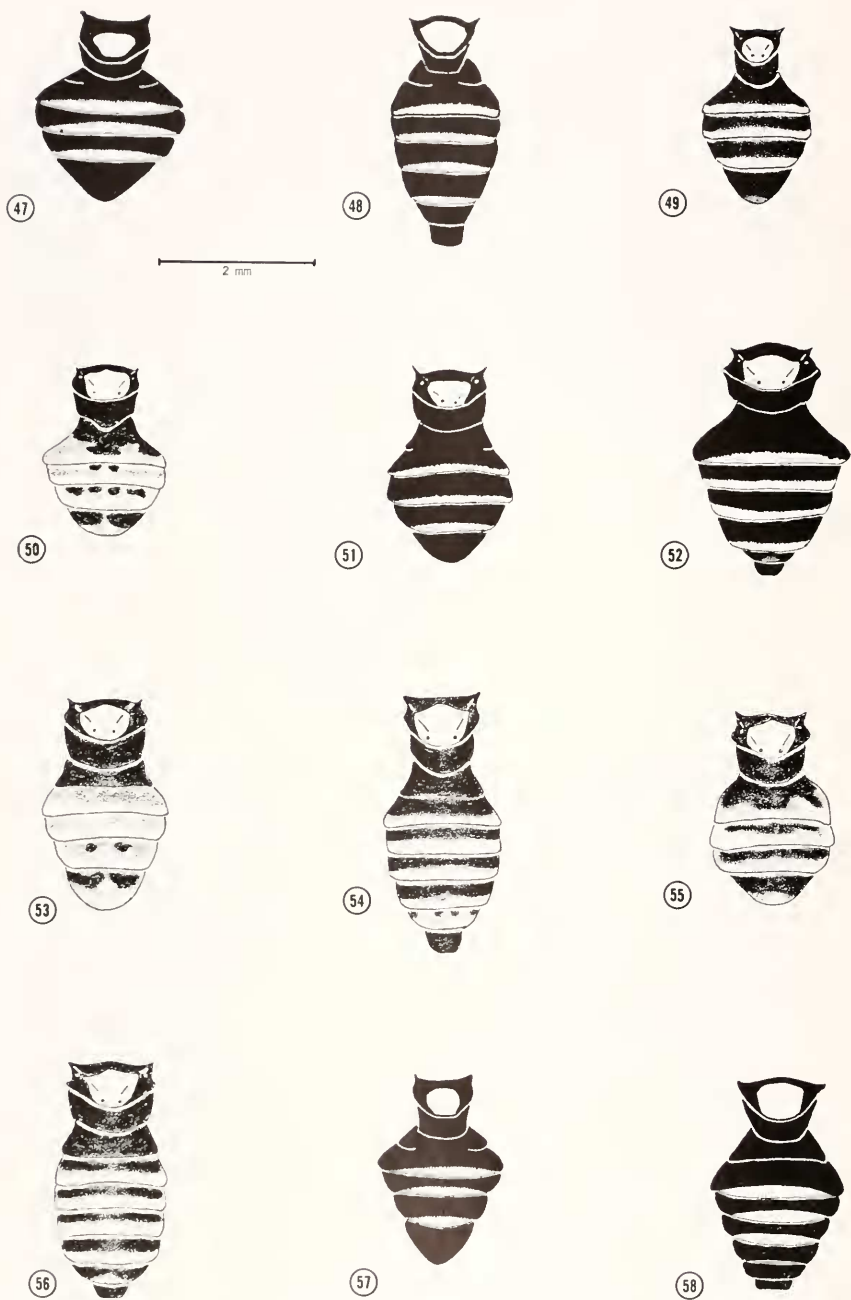
Figures 32–37. Lateral view of head of *Rhagoletis* species. Fig. 32. *R. cingulata* (Loew), ♂, Mass. (also typical of *indifferens*, *osmanthi* and *chiananthi*). Fig. 33. *R. persimilis* n. sp., ♂, B.C., Can. Fig. 34. *R. tabellaria* (Fitch), ♂, Mass. Fig. 35. *R. berberis* Curran, ♂, Ore. Fig. 36. *R. juniperina* Marcovitch, ♂, Mass. Fig. 37. *R. ribicola* Daane, ♂, Ore.



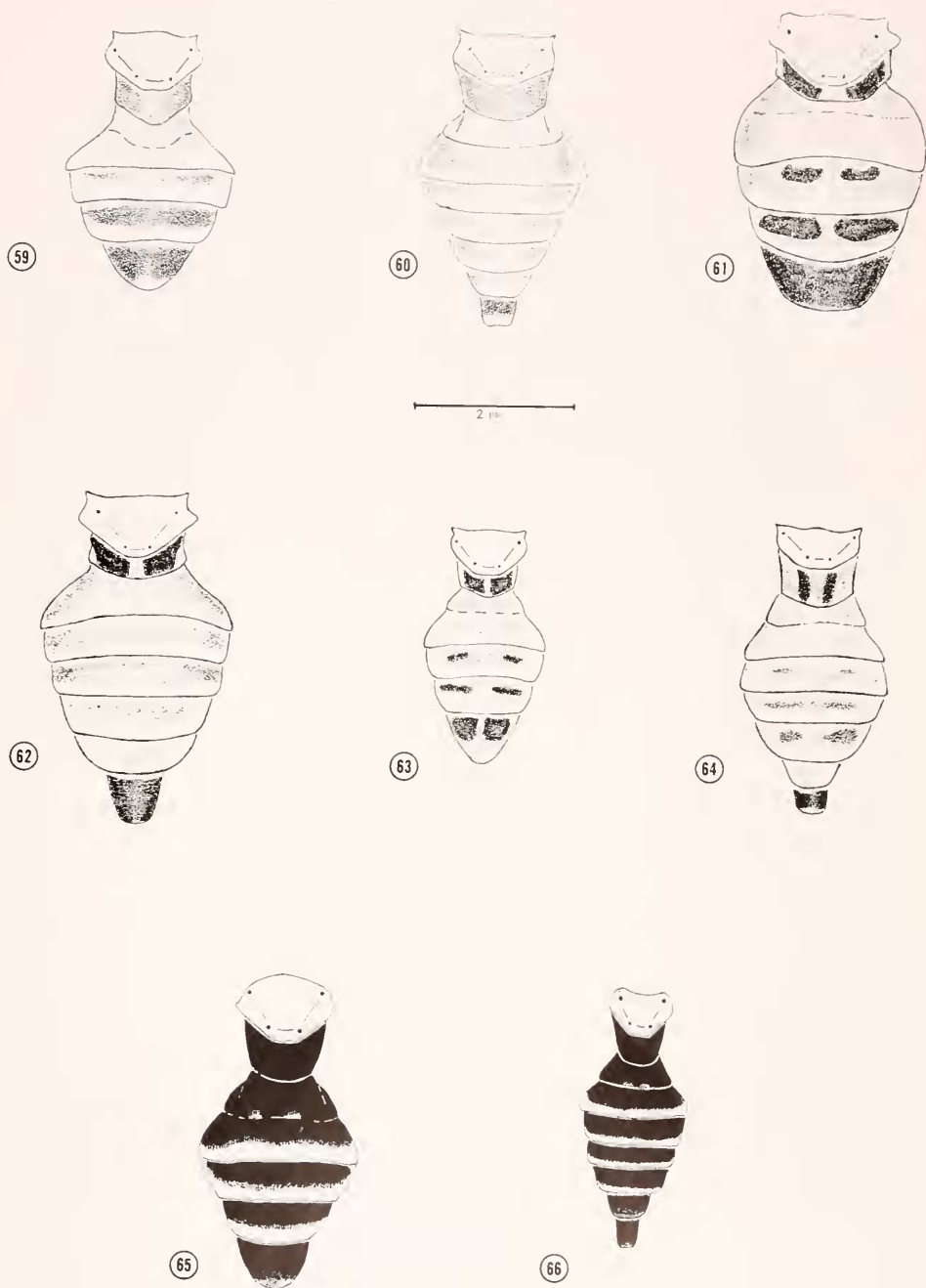
Figures 38-41. Lateral view of head of *Rhagoletis* species. Fig. 38. *R. basiala* (Osten Sacken), ♂, Mass. Fig. 39. *R. cerasi* (Linn.), ♂, France. Fig. 40. *R. fausta* (Osten Sacken), ♂, N.H. Fig. 41. *R. striatella* van der Wulp, ♂, Mexico.



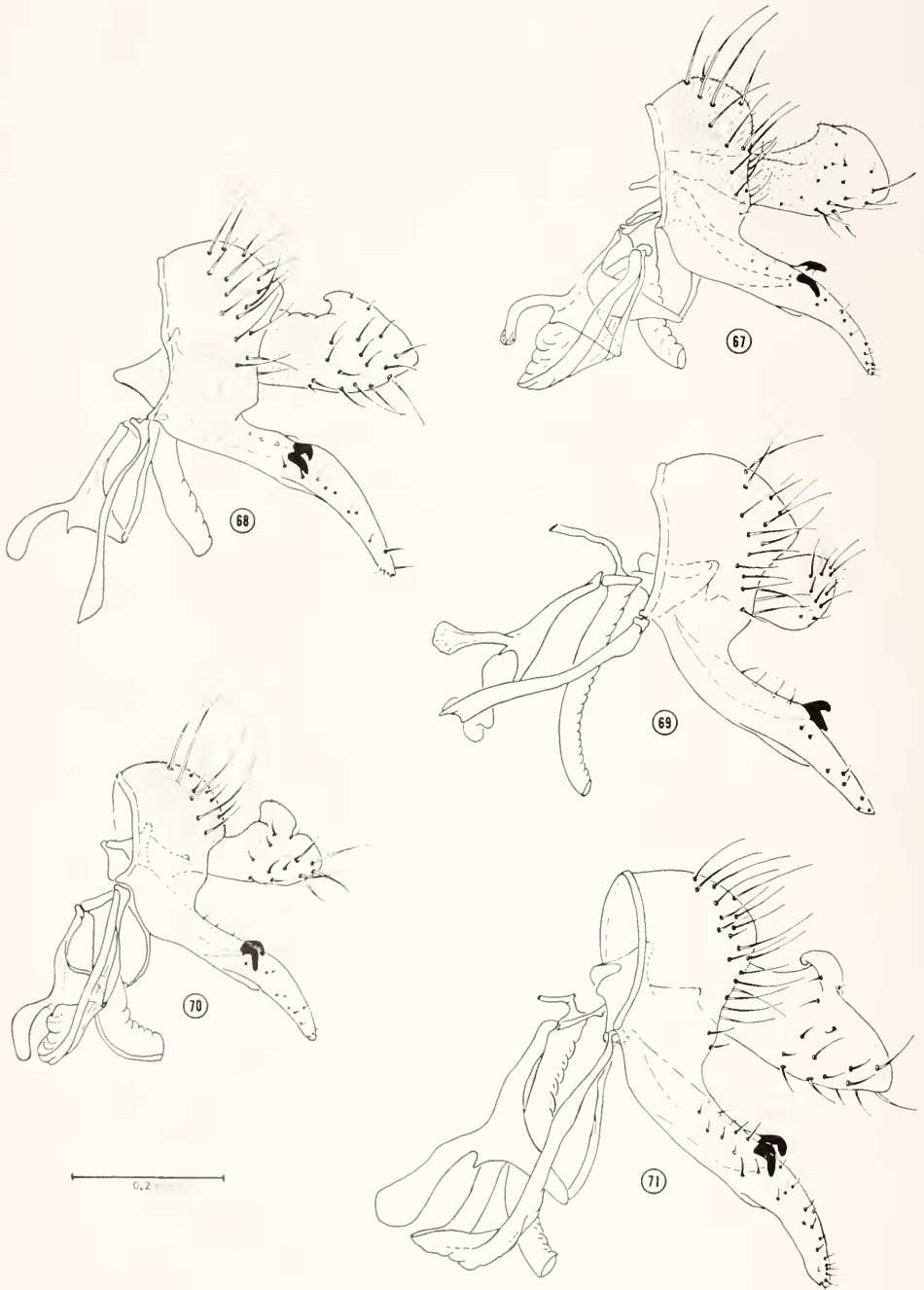
Figures 42-46. Dorsal view of thorax of *Rhagoletis* species. Fig. 42. *R. striatella* von der Wulp, ♂, Mexico. Fig. 43. *R. ebbettsi* n. sp., ♀ (holotype), Calif. Fig. 44. *R. juniperina* Marcovitch, ♂, Mass. Fig. 45. *R. pomonella* (Walsh), ♂, Mass. Fig. 46. *R. tabellaria* (Fitch), ♂, Mass. [also typical of *persimilis*, *ribicola* and *berberis*].



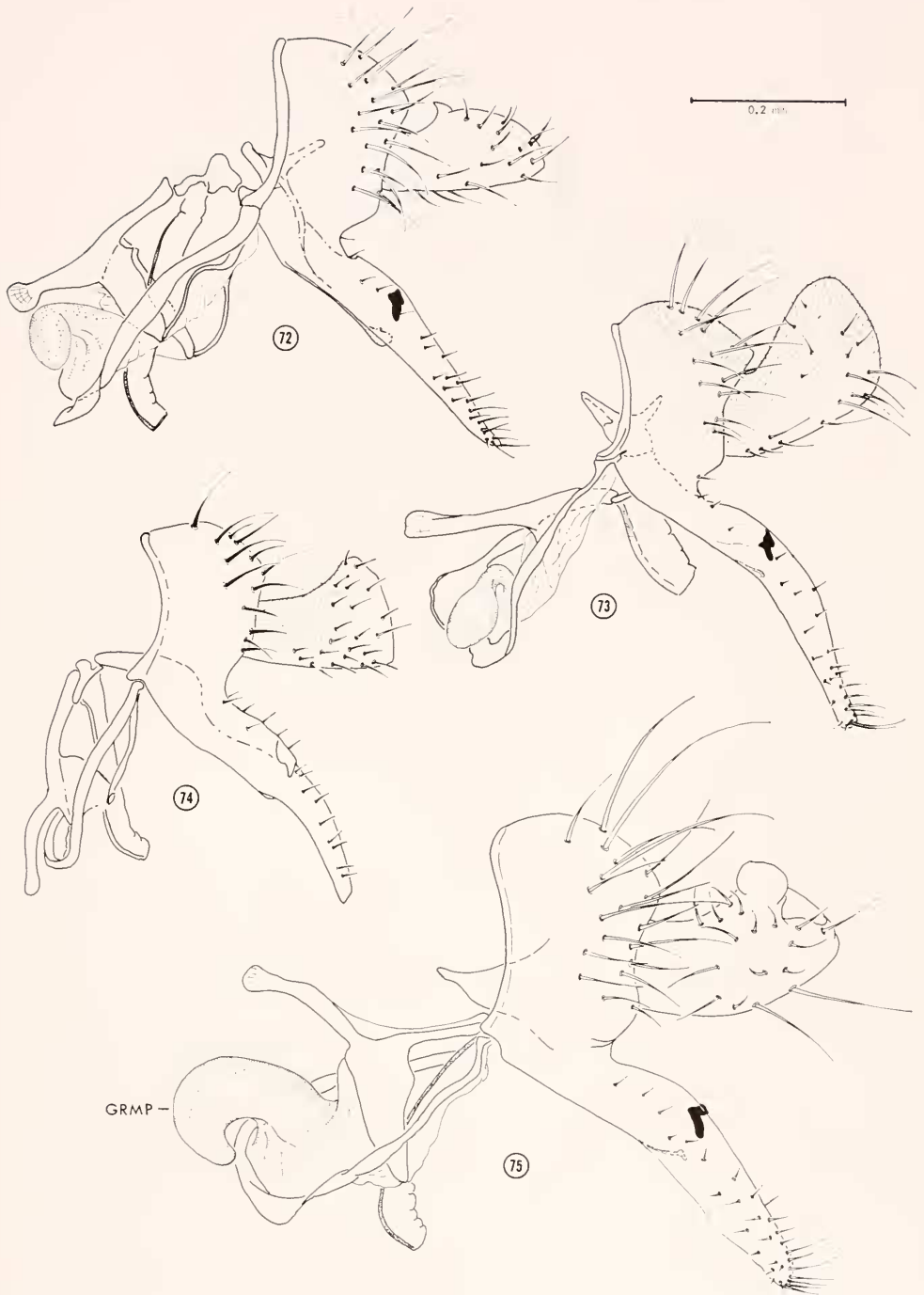
Figures 47-58. Dorsal view of abdomen of *Rhagoletis* species. Fig. 47. *R. pomonella* (Walsh), ♂, Mass. Fig. 48. *R. pomonella* (Walsh), ♀, Mass. Fig. 49. *R. cingulata* (Loew), ♂, N.Y. Fig. 50. *R. cingulata* (Loew), ♂, Fla. Fig. 51. *R. indifferens* Curran, ♂, Ore. Fig. 52. *R. indifferens* Curran, ♀, Ore. Fig. 53. *R. osmanthi* n. sp., ♂, Fla. Fig. 54. *R. osmanthi* n. sp., ♀, Fla. Fig. 55. *R. chionanthi* n. sp., ♂, Fla. Fig. 56. *R. chionanthi* n. sp., ♀, Fla. Fig. 57. *R. tabellaria* (Fitch), ♂, Wash. (also typical of *juniperina*, *persimilis*, *ribicola* and *berberis*). Fig. 58. *R. tabellaria* (Fitch), ♀, Wash. (also typical of *juniperina*, *persimilis*, *ebbettsi*, *ribicola* and *berberis*).



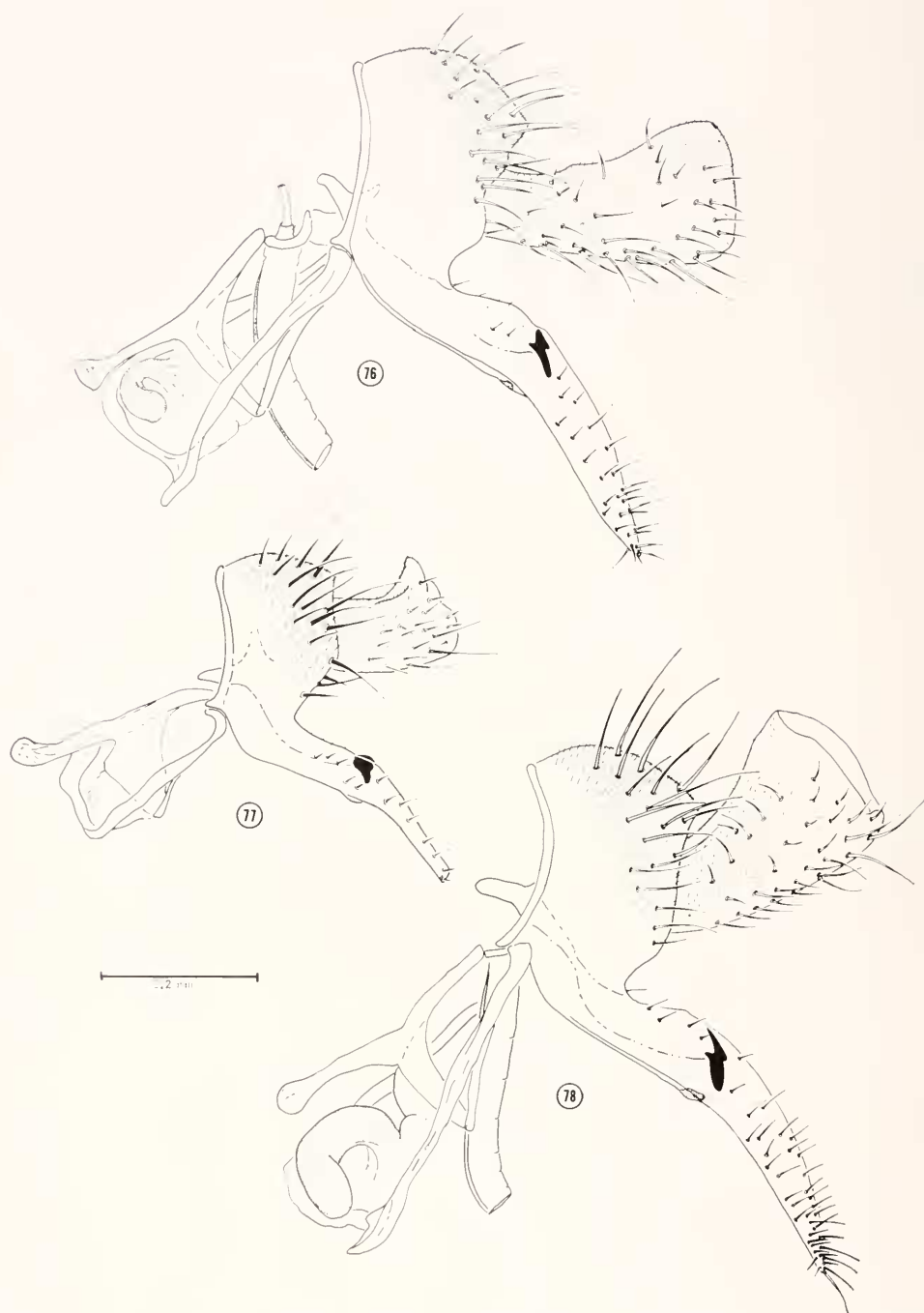
Figures 59-66. Dorsal view of abdomen of *Rhagoletis* species. Fig. 59. *R. suavis* (Loew), ♂, Mass. Fig. 60. *R. suavis* (Loew), ♀, Mass. Fig. 61. *R. zoqui* n. sp., ♂, Hidalgo, Mex. Fig. 62. *R. zoqui* n. sp., ♀, Hidalgo, Mex. Fig. 63. *R. completa* Cresson, ♂, Calif. Fig. 64. *R. completa* Cresson, ♀, Calif. Fig. 65. *R. boycei* Cresson, ♂, Ariz. Fig. 66. *R. boycei* Cresson, ♀, Ariz.



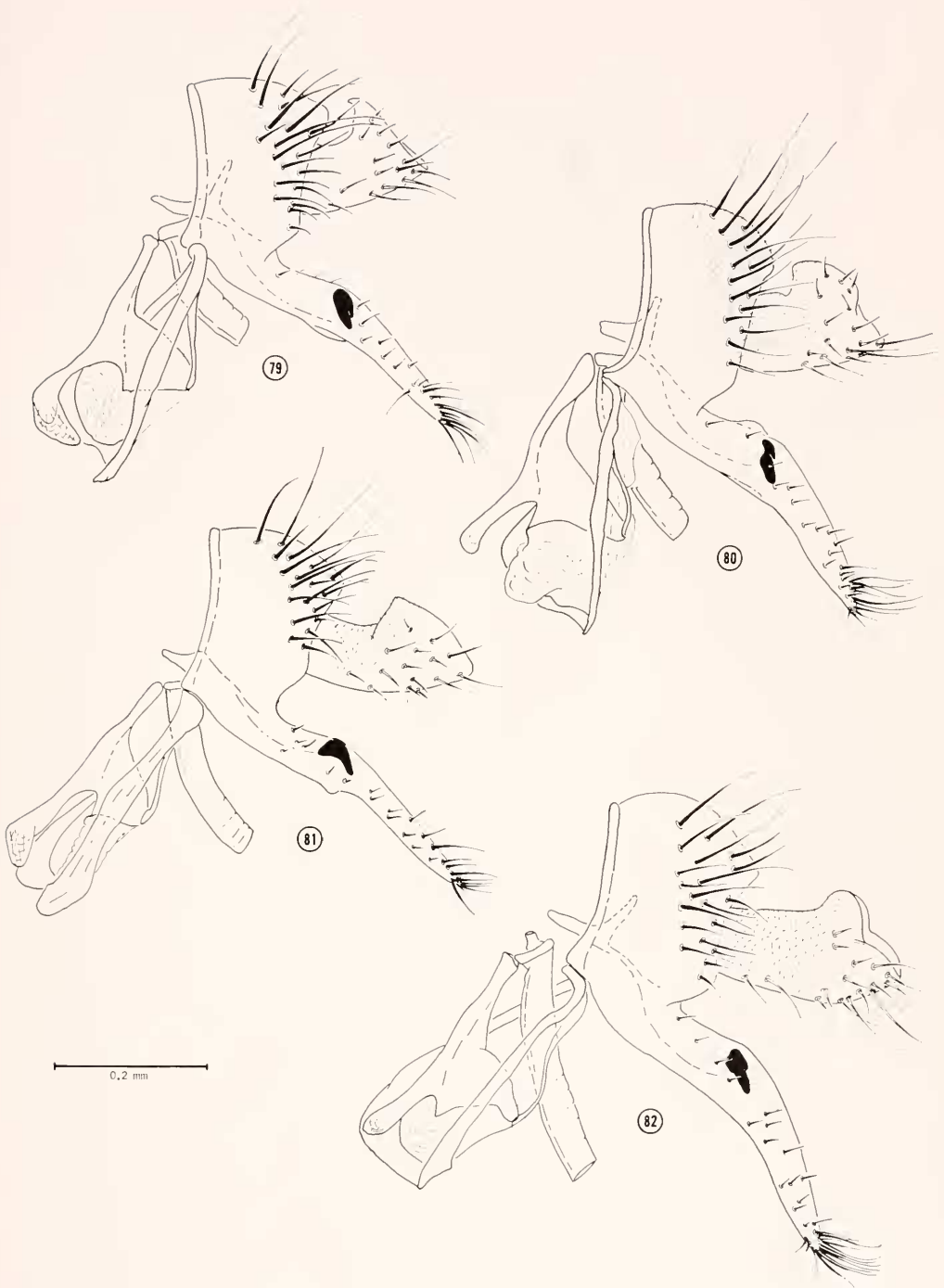
Figures 67–71. Lateral view of male genitalia of *Rhagoletis* species. Fig. 67. *R. mendax* Curran, Maine. Fig. 68. *R. carnivora* n. sp., Moss. Fig. 69. *R. zephyria* Snow, Ore. Fig. 70. *R. mendax* Curran, Fla. Fig. 71. *R. pomonella* (Walsh), Moss.



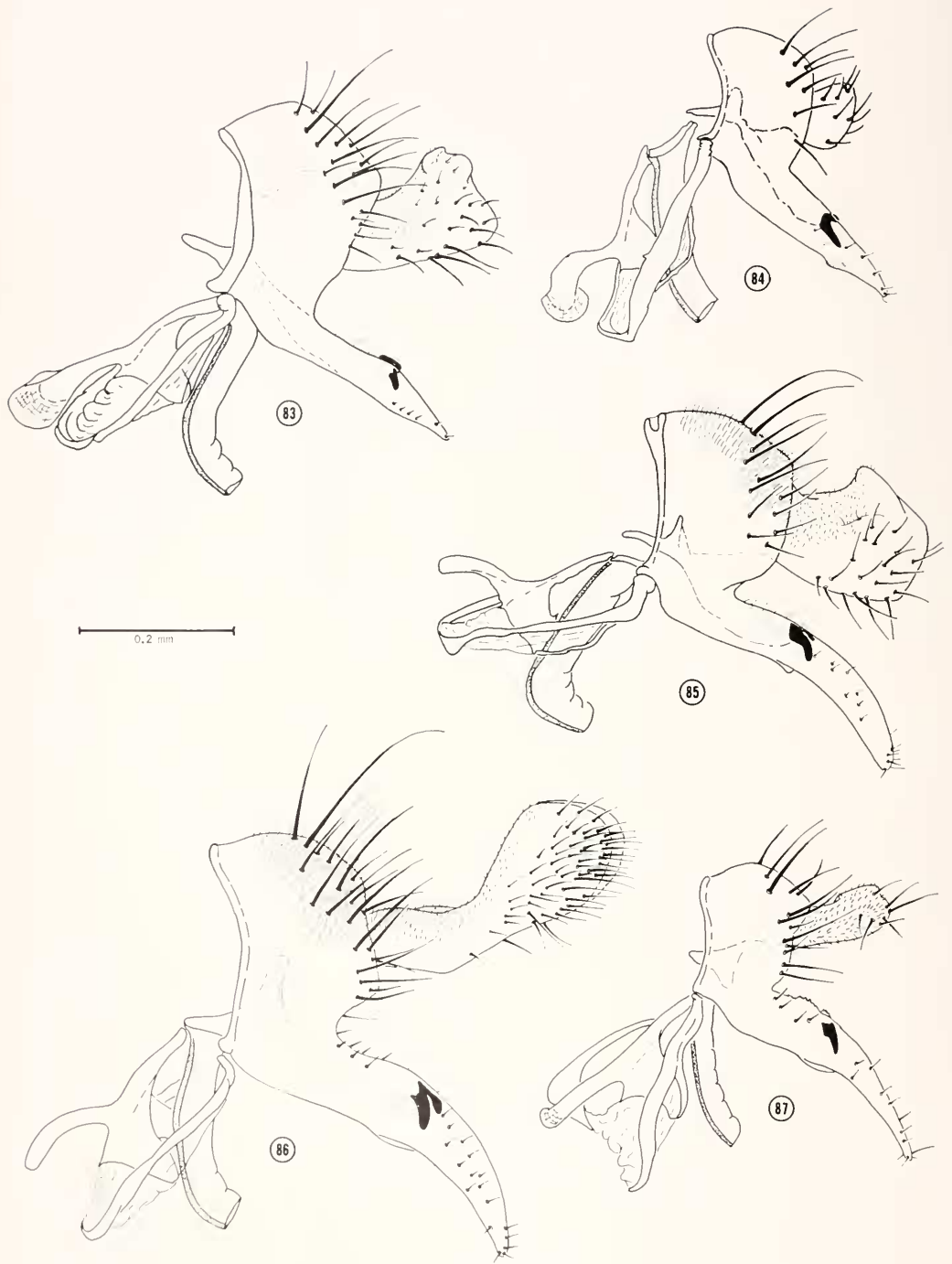
Figures 72-75. Lateral view of male genitalia of *Rhagoletis* species. Fig. 72. *R. juglandis* Cresson, Ariz. Fig. 73. *R. completa* Cresson, Calif. Fig. 74. *R. fausta* (Osten Sacken), N.H. Fig. 75. *R. suavis* (Loew), Mass. (GRMP, genital ring membrane pouch).



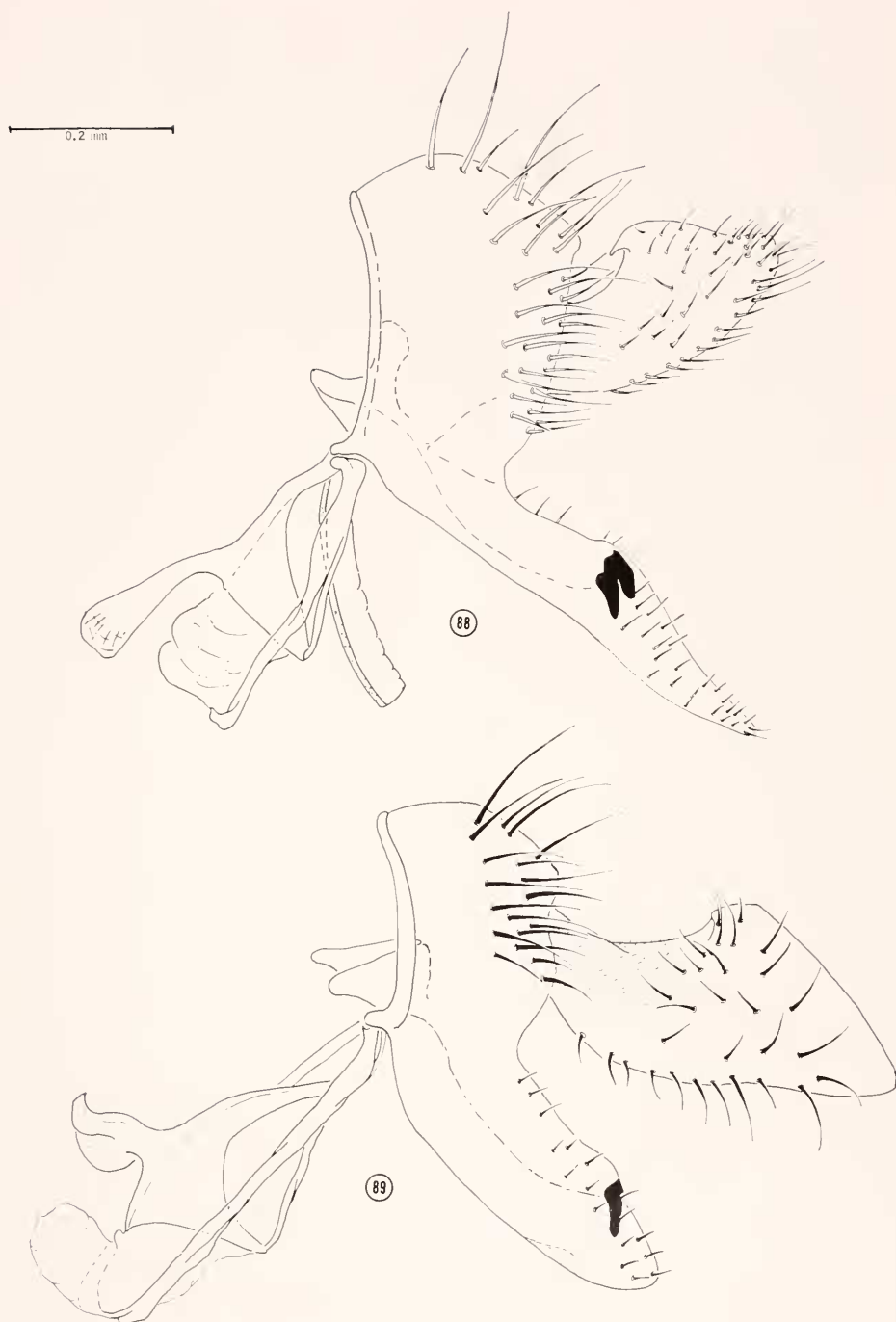
Figures 76–78. Lateral view of male genitalia of *Rhagoletis* species. Fig. 76. *R. boycei* Cresson, Ariz. Fig. 77. *R. cerasi* (Linn.), France. Fig. 78. *R. zoqui* n. sp., Hidalgo, Mex.



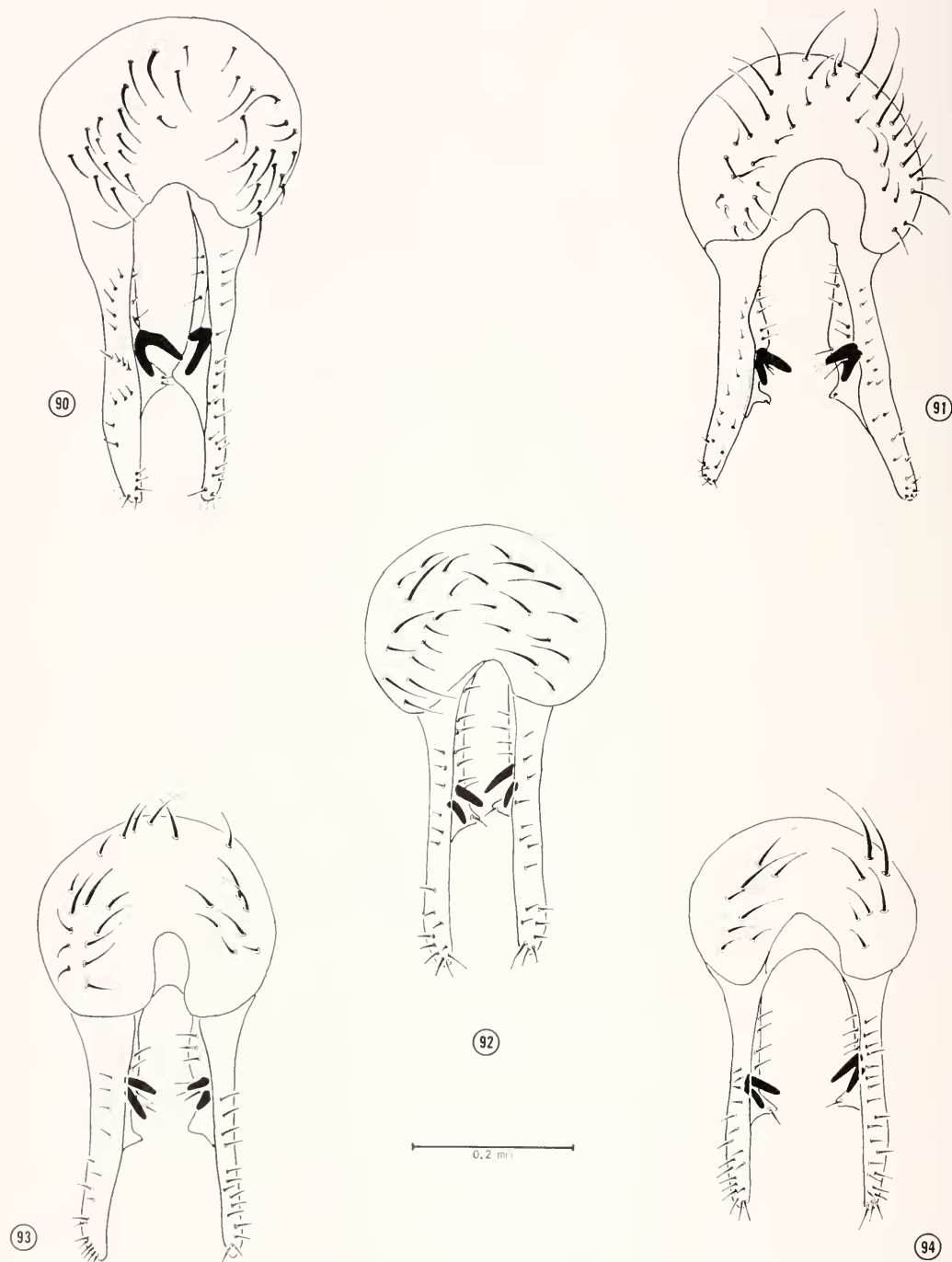
Figures 79-82. Lateral view of male genitalia of *Rhagoletis* species. Fig. 79. *R. cingulata* (Loew), Mass. Fig. 80. *R. chiananthi* n. sp., Fla. Fig. 81. *R. indifferens* Curran, Calif. Fig. 82. *R. osmanthi* n. sp., Fla.



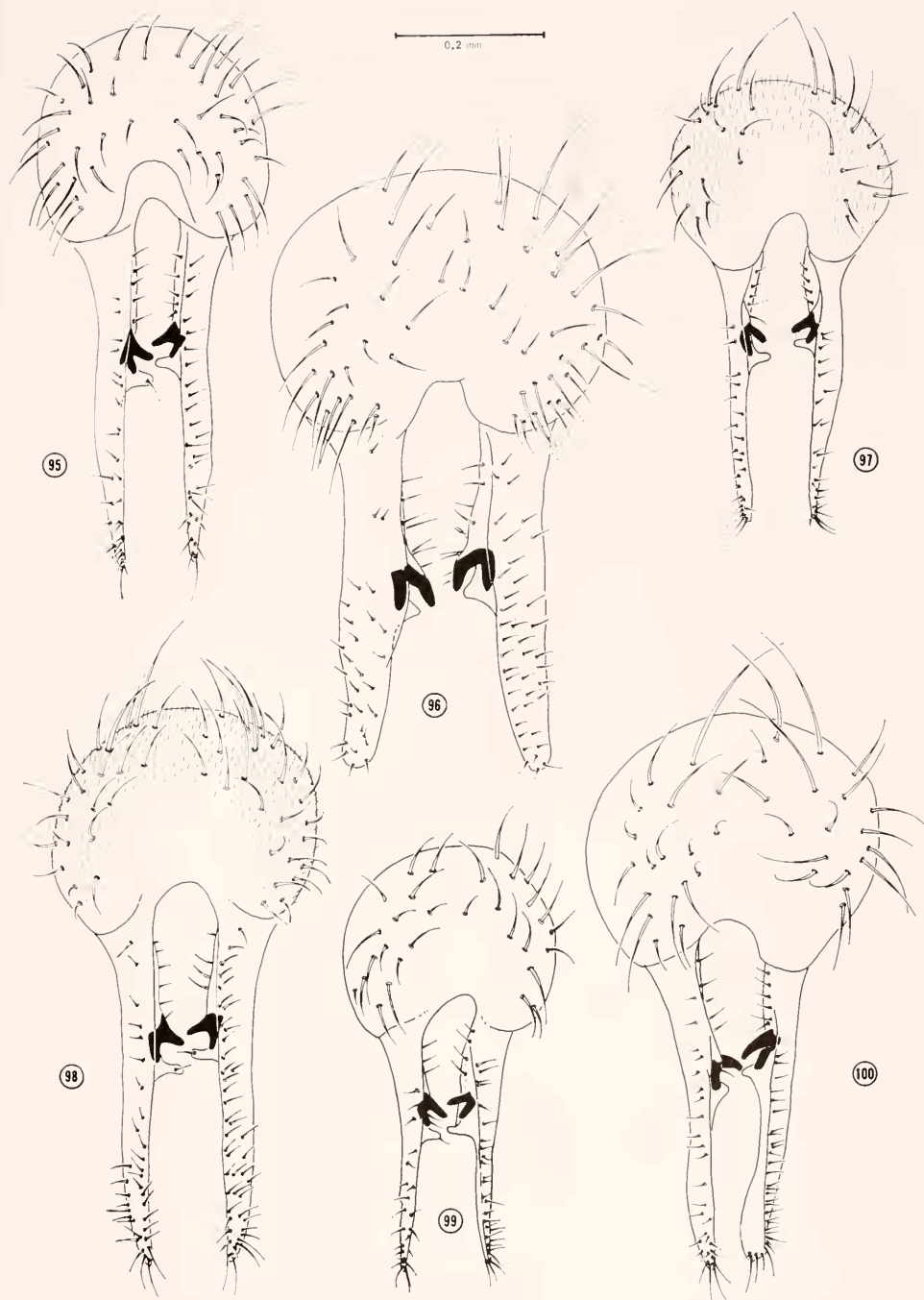
Figures 83–87. Lateral view of male genitalia of *Rhogaletis* species. Fig. 83. *R. juniperina* Morcovitch, Moss. Fig. 84. *R. ribicola* Doane, Ore. Fig. 85. *R. tabellaria* (Fitch), Moss. Fig. 86. *R. persimilis* n. sp., B.C., Can. Fig. 87. *R. berberis* Curran, Ore.



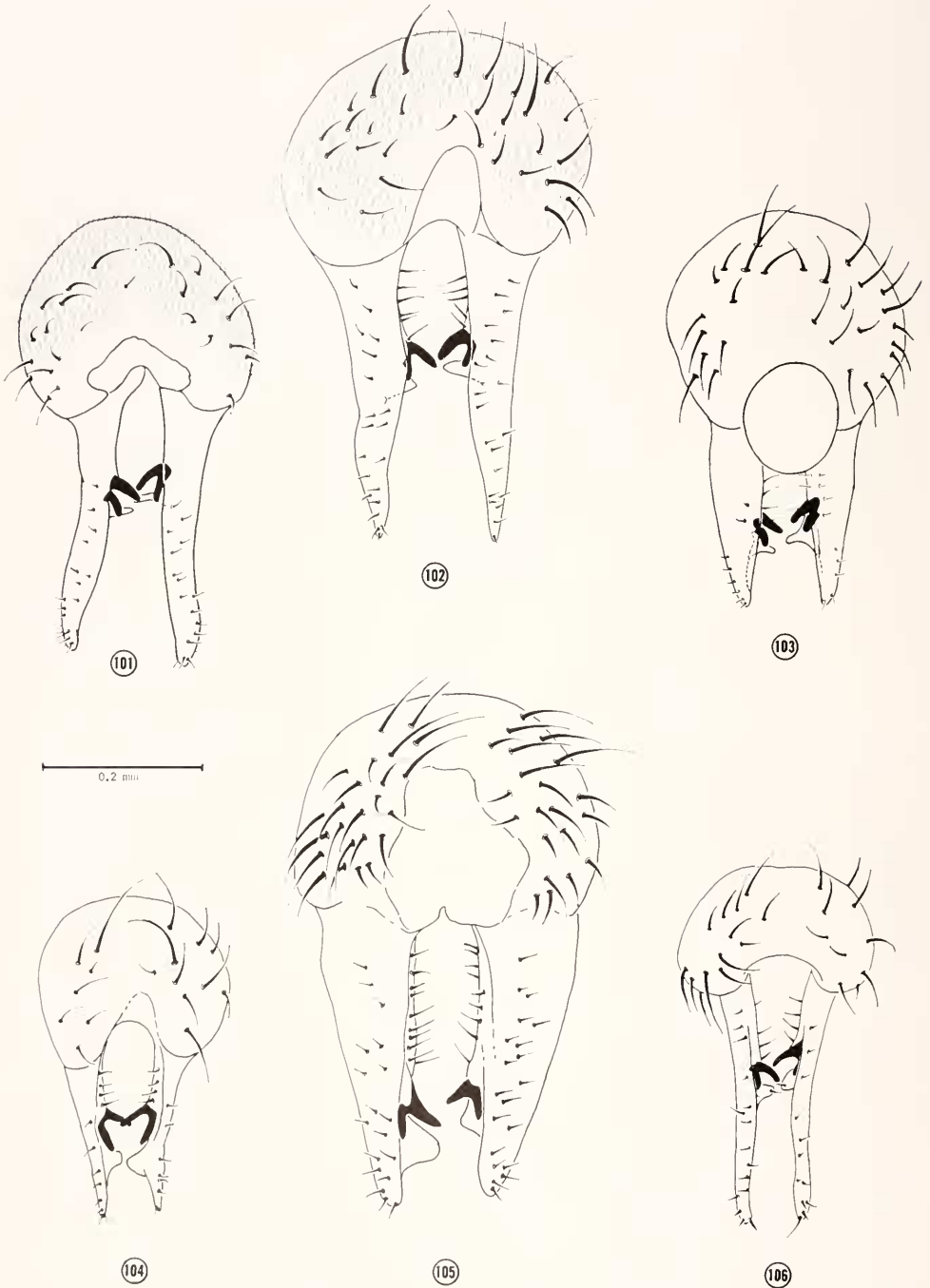
Figures 88–89. Lateral view of male genitalia of *Rhagoletis* species. Fig. 88. *R. basiola* (Cresson), Mass. Fig. 89. *R. striatella* van der Wulp, Mexico.



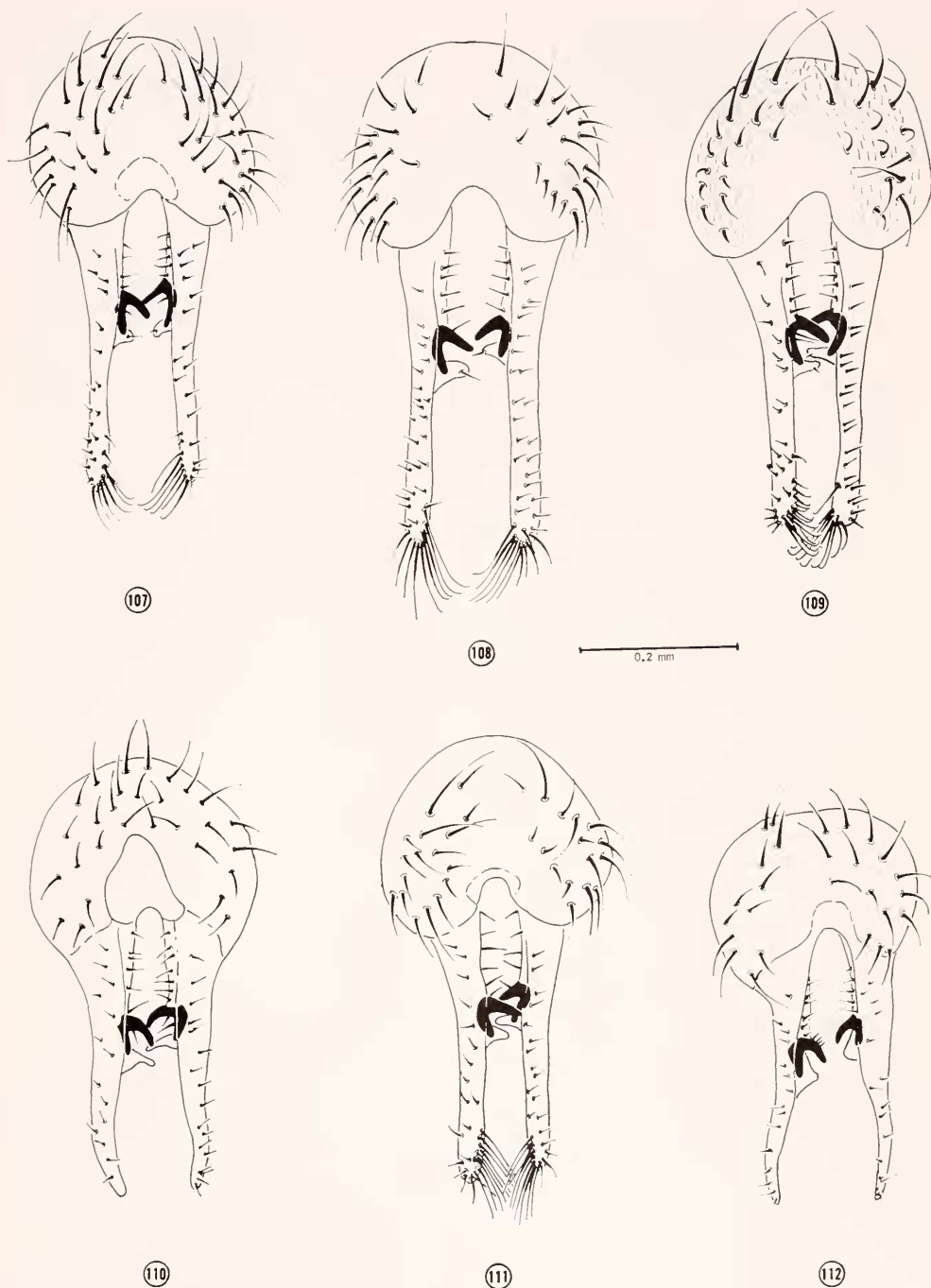
Figures 90–94. Posterior view of male genitalia of *Rhagaletis* species. Fig. 90. *R. pomanella* (Walsh), Mass. Fig. 91. *R. zephyria* Snow, Calif. Fig. 92. *R. cornivora* n. sp., Mass. Fig. 93. *R. mendax* Curran, Maine. Fig. 94. *R. mendax* Curran, Fla.



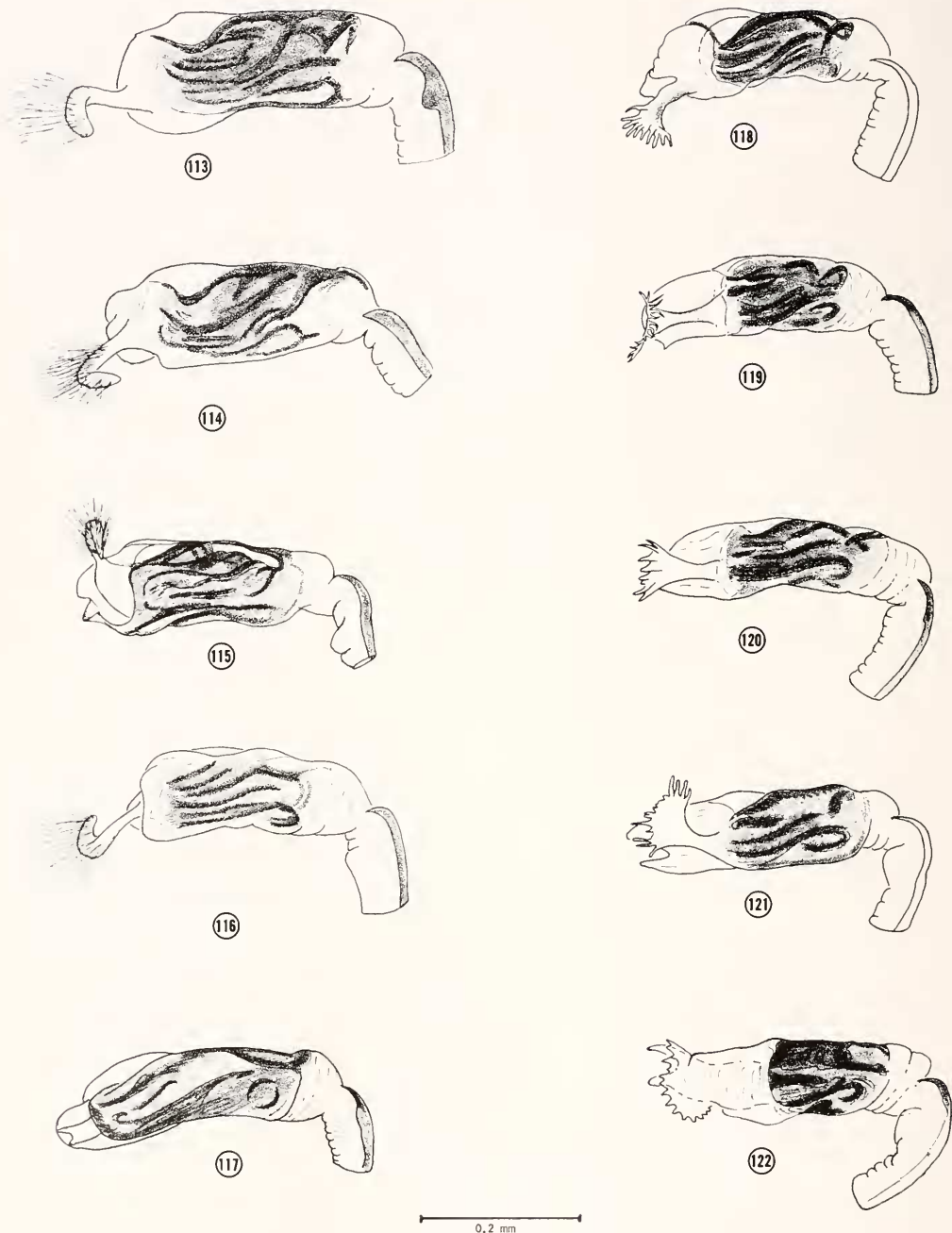
Figures 95–100. Posterior view of male genitalia of *Rhagoletis* species. Fig. 95. *R. boycei* Cresson, Ariz. Fig. 96. *R. basiola* (Osten Sacken), Mass. Fig. 97. *R. completa* Cresson, Calif. Fig. 98. *R. zaqui* n. sp., Hidalgo, Mex. Fig. 99. *R. juglandis* Cresson, Ariz. Fig. 100. *R. suavis* (Loew), Mass.



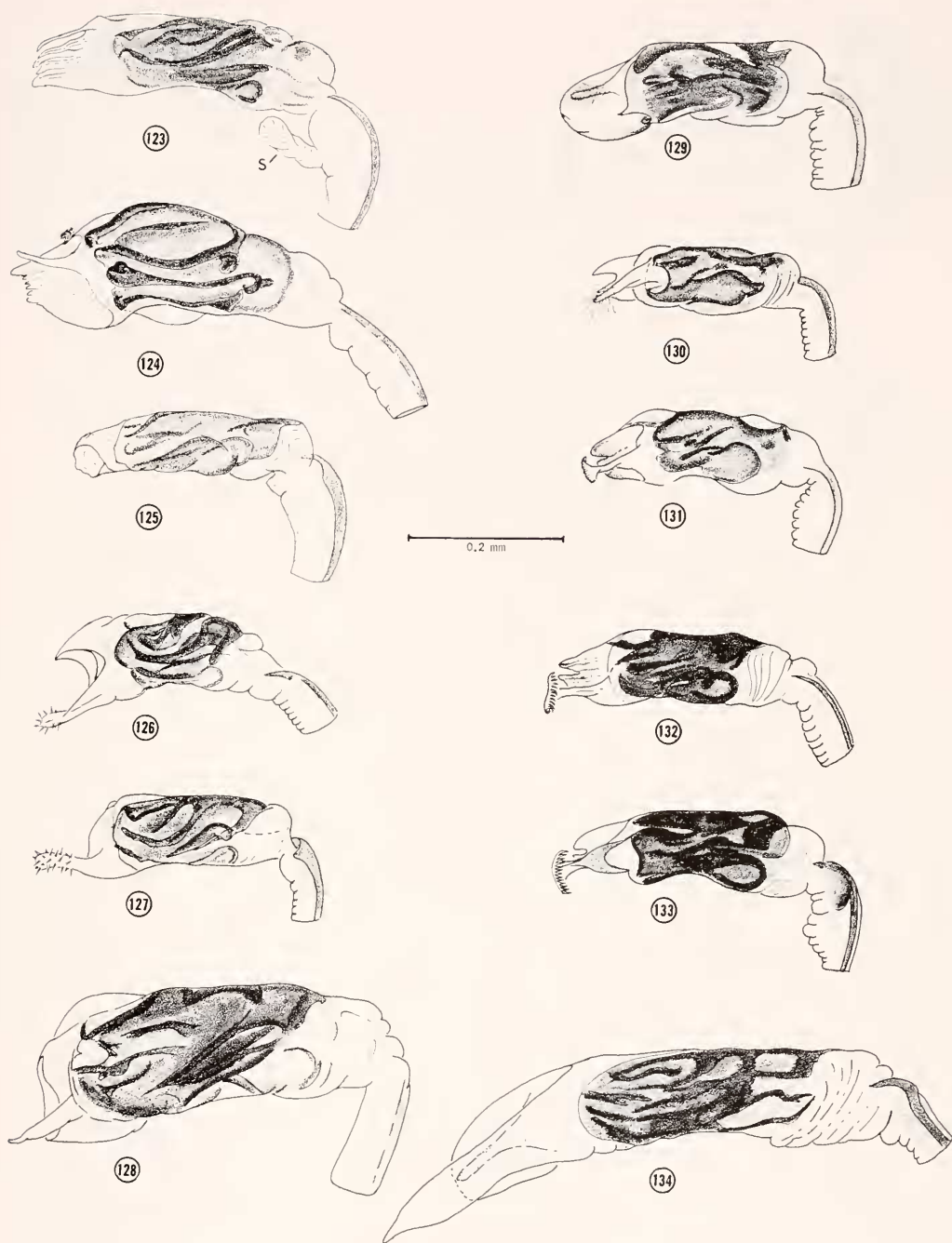
Figures 101–106. Posterior view of male genitalia of *Rhagoletis* species. Fig. 101. *R. tabellaria* (Fitch), Mass. Fig. 102. *R. persimilis* n. sp., B.C., Can. Fig. 103. *R. juniperina* Marcavitch, Mass. Fig. 104. *R. ribicola* Doane, Ore. Fig. 105. *R. striatella* van der Wulp, Mexico. Fig. 106. *R. berberis* Curran, Ore.



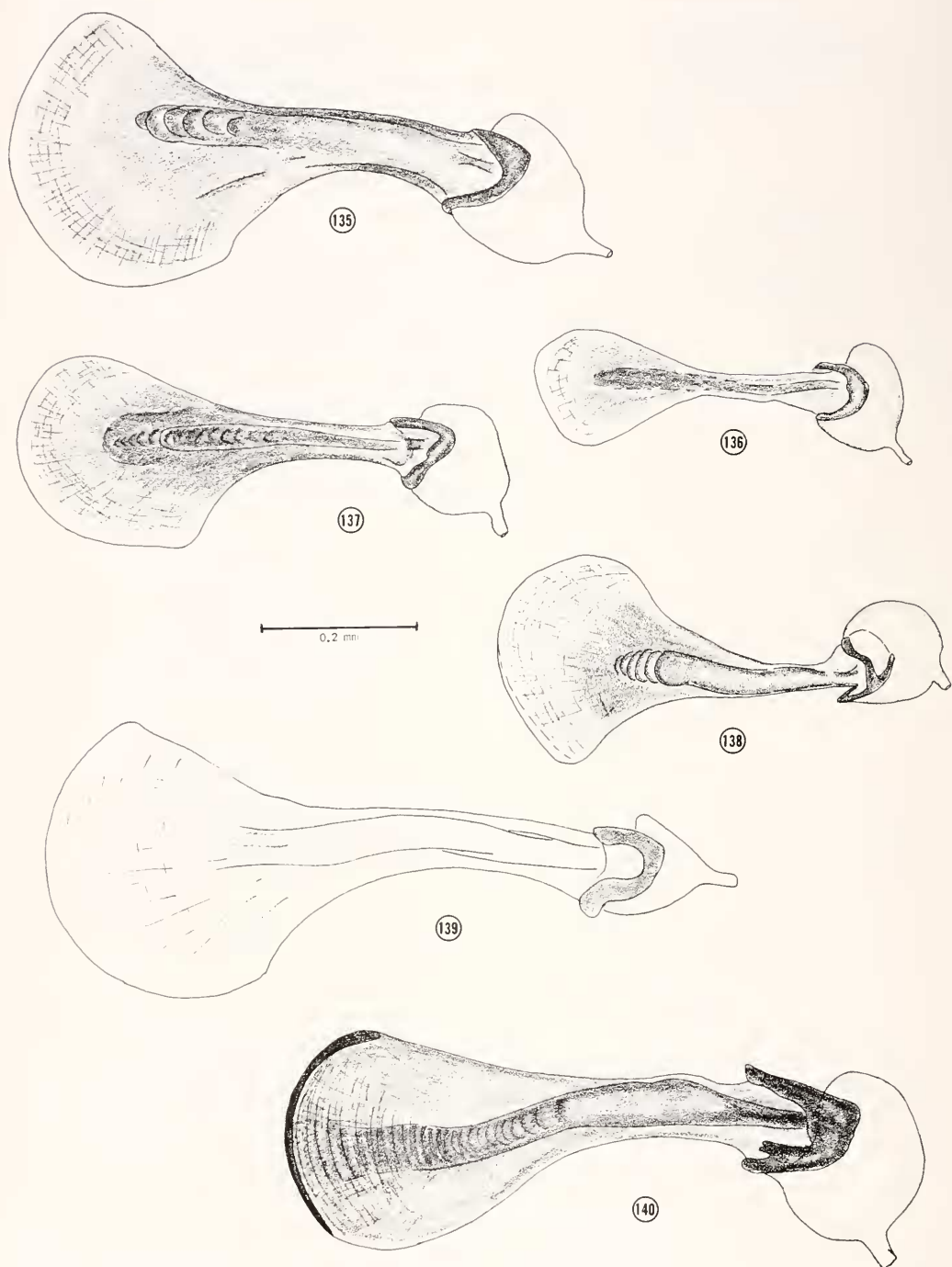
Figures 107–112. Posterior view of male genitalia of *Rhagoletis* species. Fig. 107. *R. indifferens* Curran, Calif. Fig. 108. *R. asmanthi* n. sp., Fla. Fig. 109. *R. chionanthi* n. sp., Fla. Fig. 110. *R. fausta* (Osten Sacken), N.H. Fig. 111. *R. cingulata* (Loew), Mass. Fig. 112. *R. cerasi* (Linn.), France.



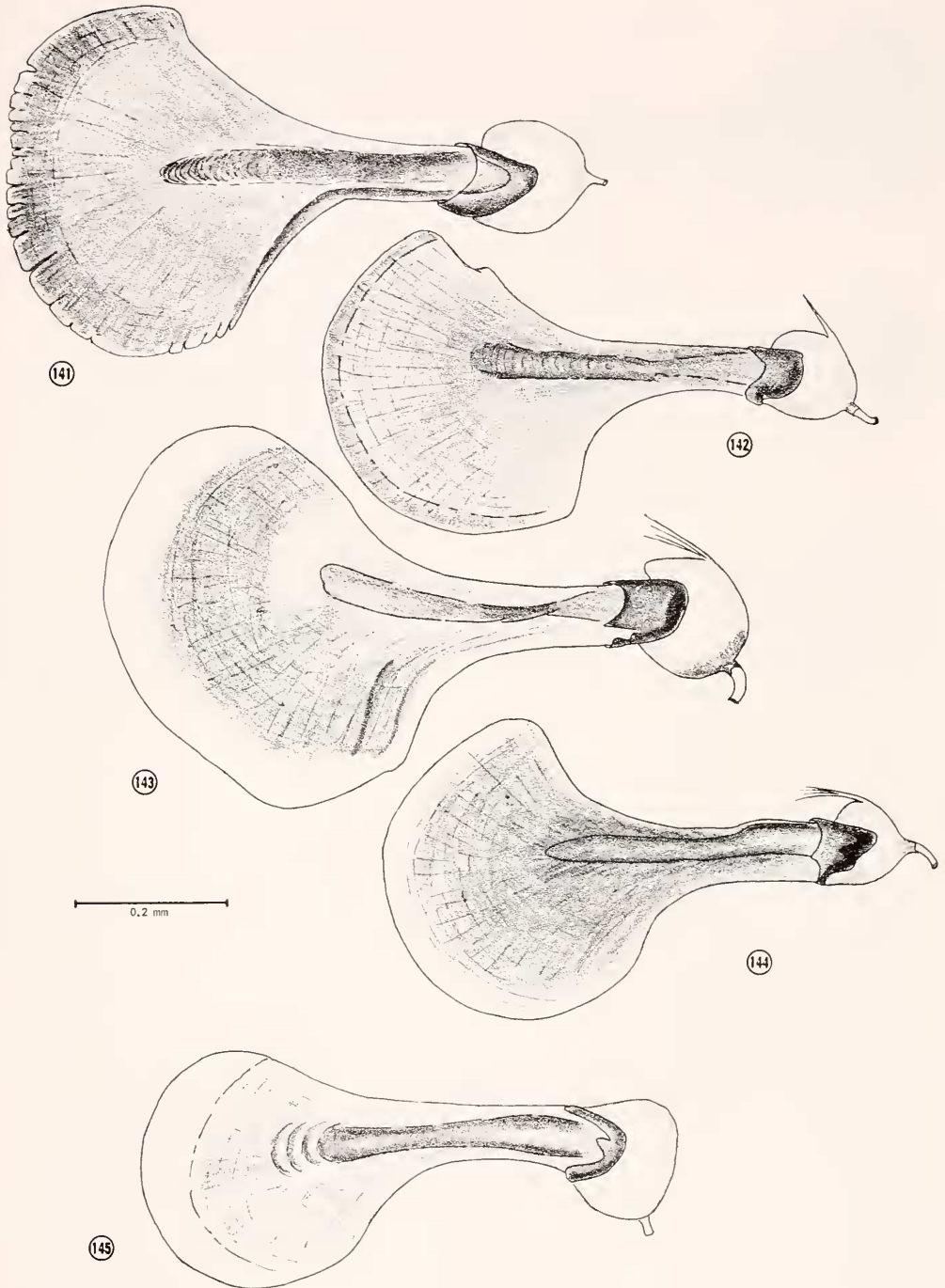
Figures 113–122. Lateral view of aedeagus of *Rhagaletis* species. Fig. 113. *R. pomonella* (Walsh), Mass. Fig. 114. *R. zephyria* Snow, Calif. Fig. 115. *R. mendax* Curran, Maine. Fig. 116. *R. cornivora* n. sp., Mass. Fig. 117. *R. fausta* (Osten Sacken), N.H. Fig. 118. *R. cingulata* (Loew), Mass. Fig. 119. *R. indifferens* Curran, Calif. Fig. 120. *R. osmanthi* n. sp., Fla. Fig. 121. *R. chionanthi* n. sp., Flo. Fig. 122. *R. cerasi* (Linn.), France.



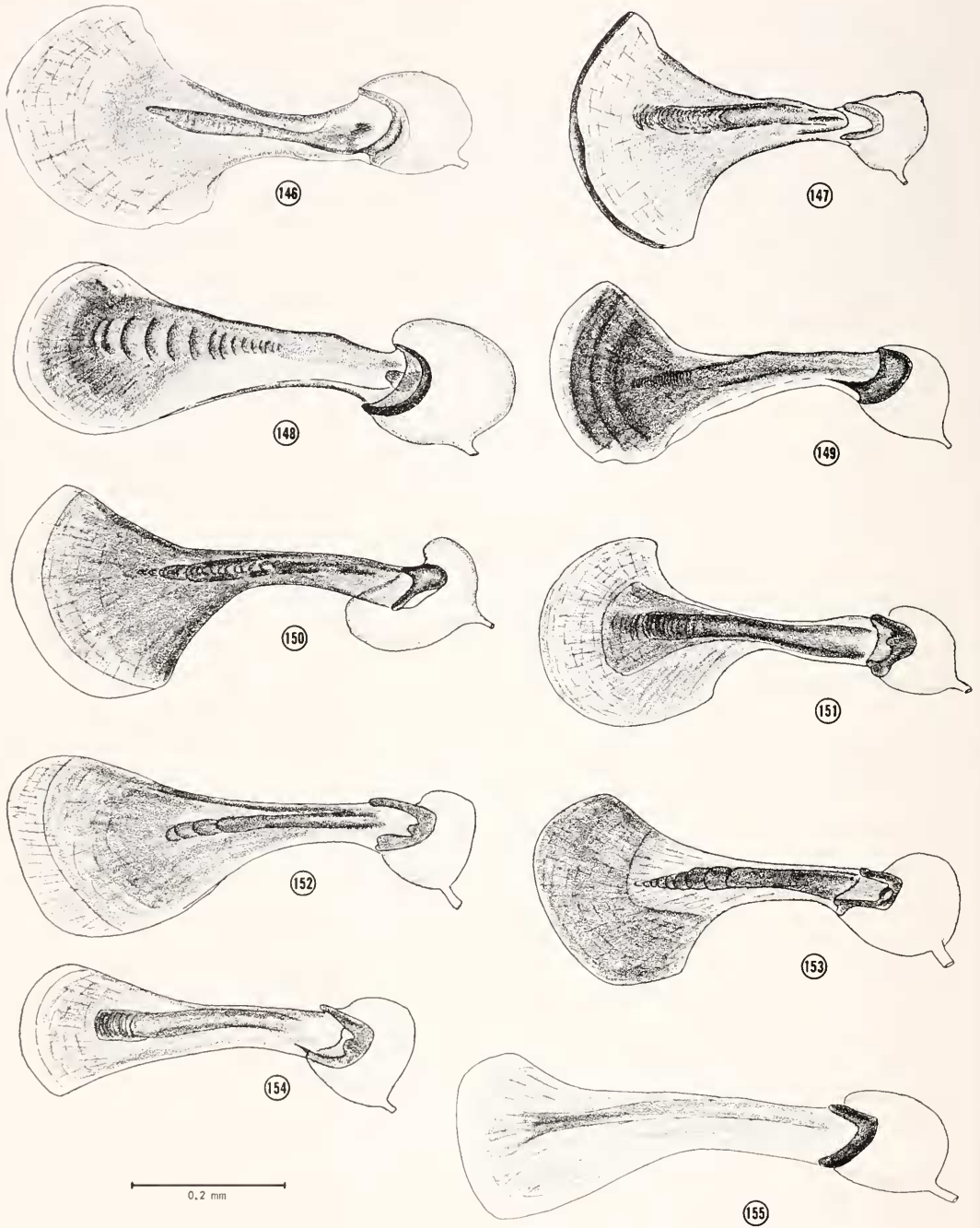
Figures 123-134. Lateral view of aedeagus of *Rhagoletis* species. Fig. 123. *R. tabellaria* (Fitch), Mass., S = tubular sac. Fig. 124. *R. persimilis* n. sp., B.C., Can. Fig. 125. *R. juniperina* Marcovitch, Mass. Fig. 126. *R. berberis* Curran, Ore. Fig. 127. *R. ribicola* Doane, Ore. Fig. 128. *R. basiala* (Osten Sacken), Mass. Fig. 129. *R. suavis* (Laew), Mass. Fig. 130. *R. juglandis* Cresson, Ariz. Fig. 131. *R. completa* Cresson, Calif. Fig. 132. *R. boycei* Cresson, Ariz. Fig. 133. *R. zoqui* n. sp., Hidalgo, Mex. Fig. 134. *R. striatella* van der Wulp, Mexico.



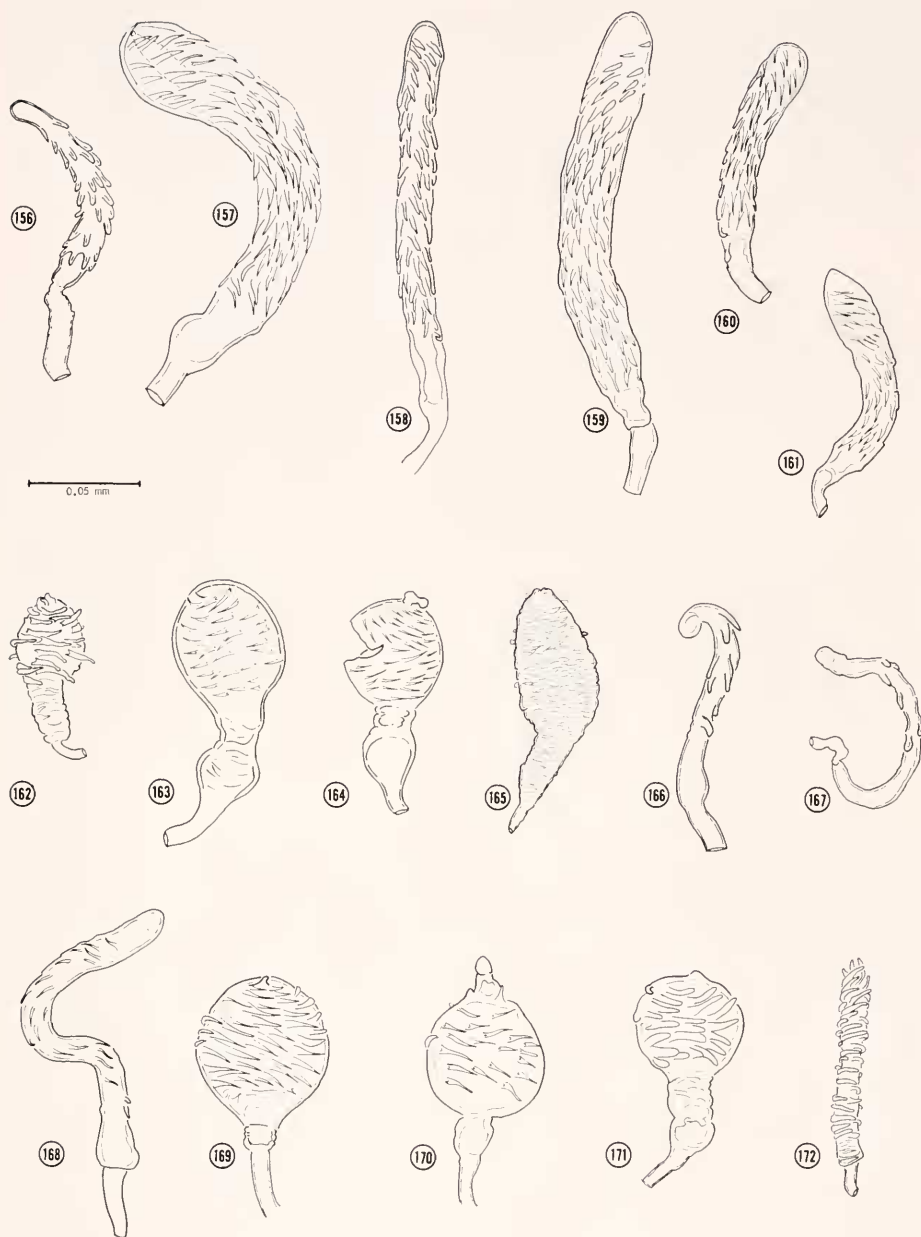
Figures 135–140. Ejaculatory apodeme of *Rhagaletis* species. Fig. 135. *R. pomonella* (Walsh), Mass. Fig. 136. *R. cornivora* n. sp., Mass. Fig. 137. *R. zephyria* Snow, Calif. Fig. 138. *R. mendax* Curran, Maine. Fig. 139. *R. basiola* (Osten Sacken), Mass. Fig. 140. *R. striatella* van der Wulp, Hidalgo, Mex.



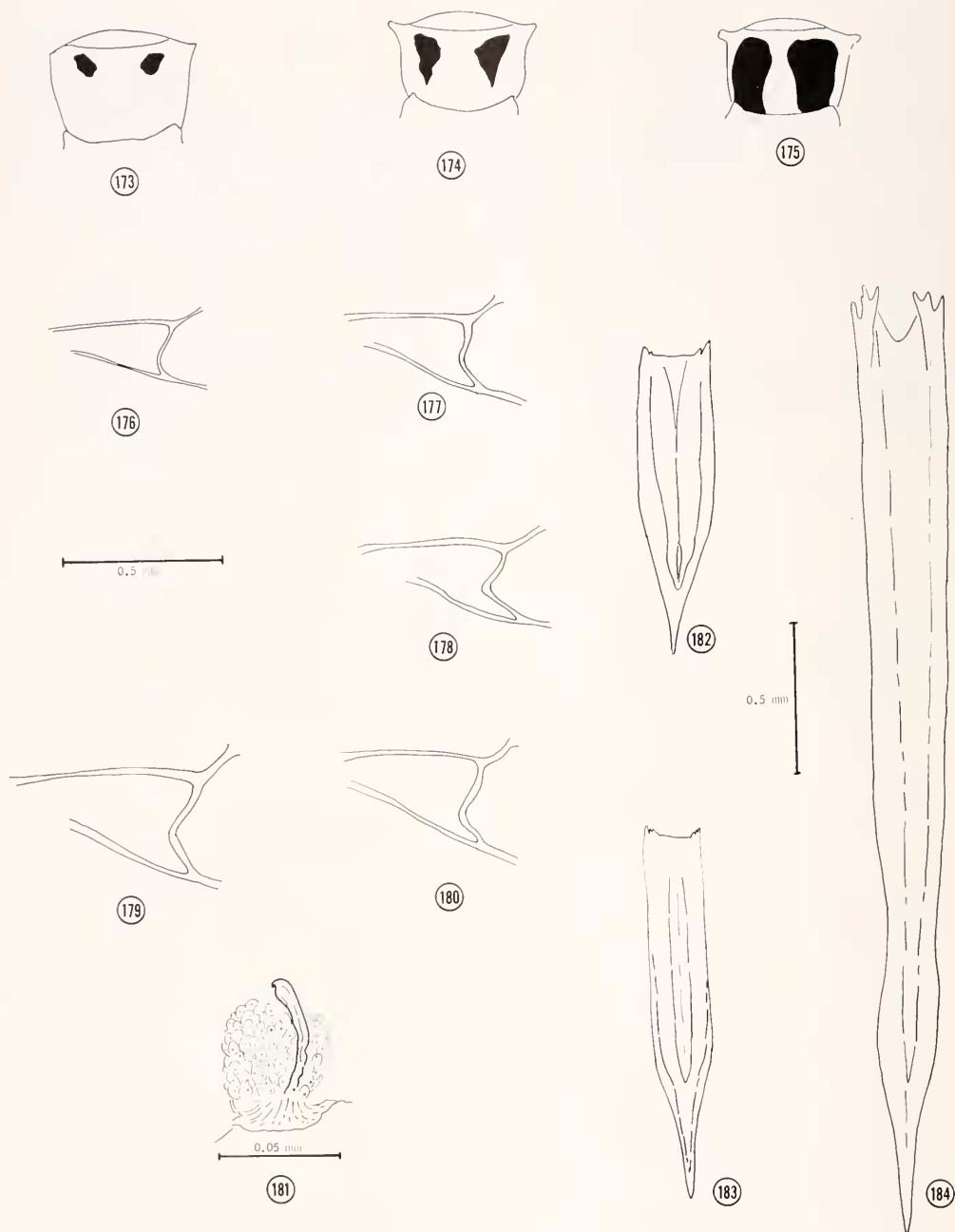
Figures 141–145. Ejaculatory apodeme of *Rhagoletis* species. Fig. 141. *R. suavis* (Loew), Moss. Fig. 142. *R. juglandis* Cresson, Ariz. Fig. 143. *R. zaqui* n. sp., Hidalgo, Mex. Fig. 144. *R. boycei* Cresson, Ariz. Fig. 145. *R. completa* Cresson, Calif.



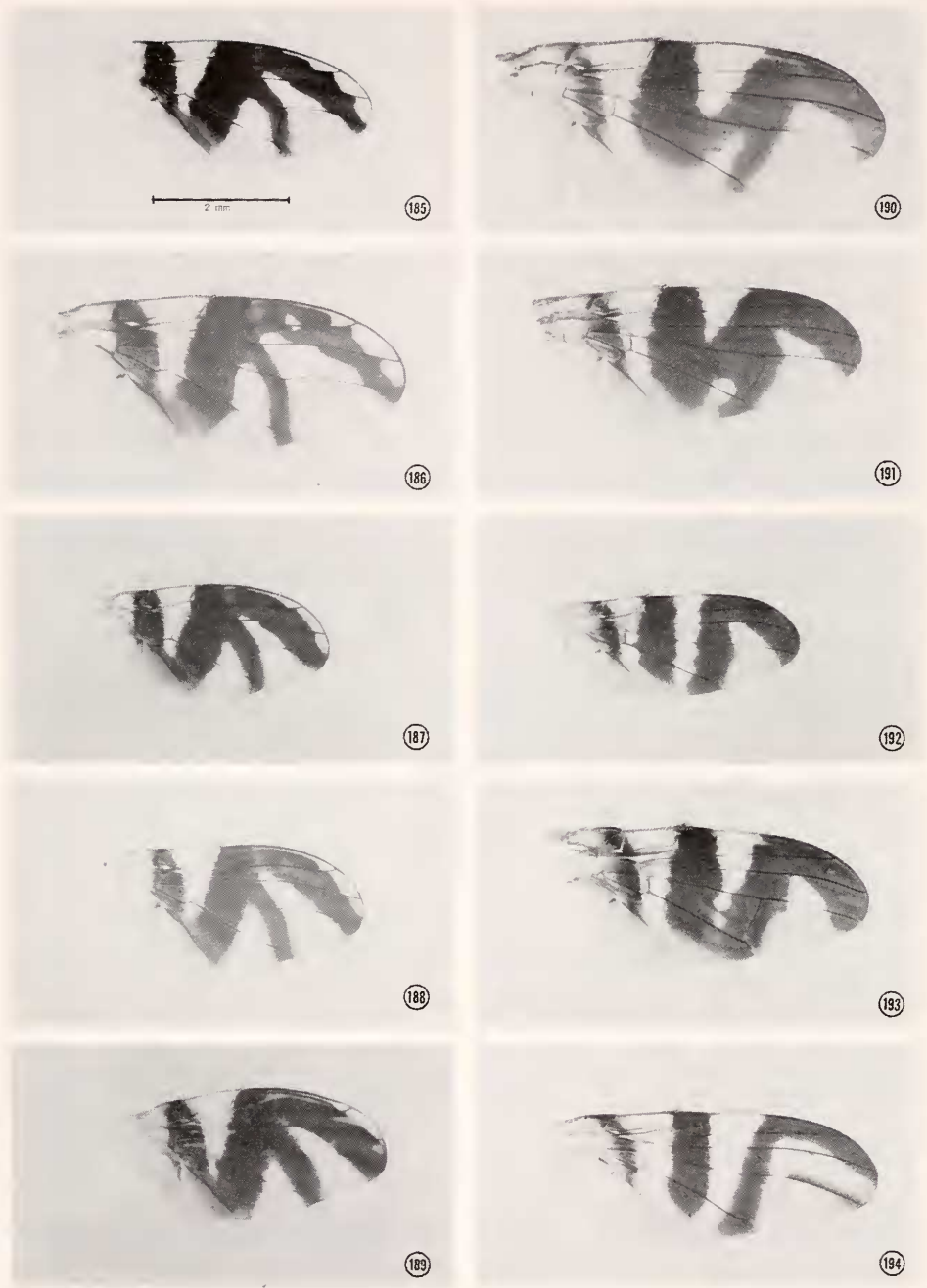
Figures 146–155. Ejaculatory apodeme of *Rhagoletis* species. Fig. 146. *R. tabellaria* (Fitch), Mass. Fig. 147. *R. ribicala* Doane, Ore. Fig. 148. *R. persimilis* n. sp., B.C., Can. Fig. 149. *R. berberis* Curran, Ore. Fig. 150. *R. juniperina* Marcovitch, Mass. Fig. 151. *R. fausta* (Osten Sacken), N.H. Fig. 152. *R. cingulata* (Loew), Mass. Fig. 153. *R. indifferens* Curran, Calif. Fig. 154. *R. chiananthi* n. sp., Fla. Fig. 155. *R. asmanthi* n. sp., Fla.



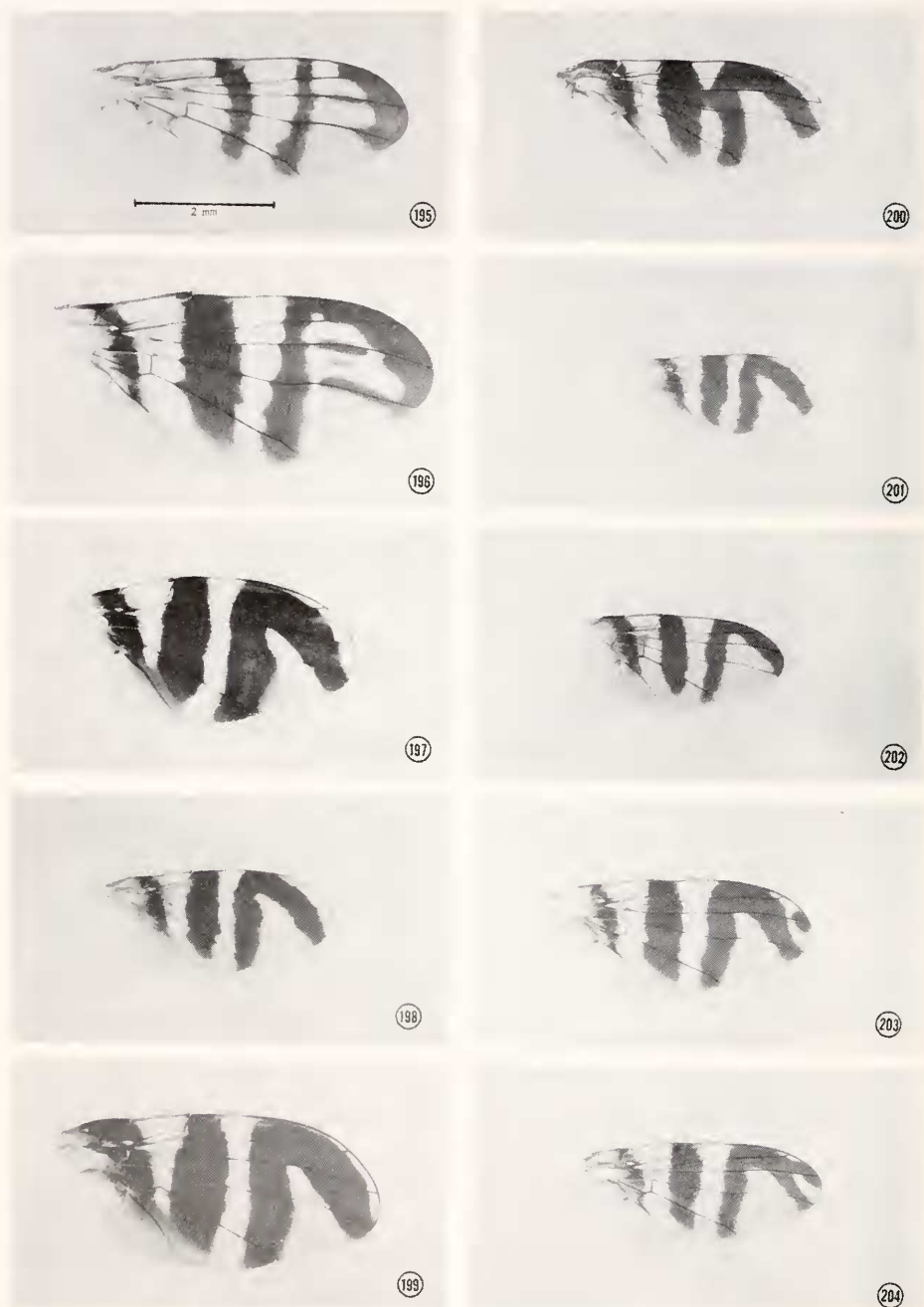
Figures 156-172. Spermathecae of *Rhagoletis* species. Fig. 156. *R. pamanella* (Walsh), Mass. (also typical of *mendax*, *zephyria* and *carnivara*). Fig. 157. *R. suavis* (Loew), Mass. Fig. 158. *R. completa* Cresson, Calif. Fig. 159. *R. zaqui* n. sp., Hidalgo, Mex. Fig. 160. *R. juglandis* Cresson, Ariz. Fig. 161. *R. boycei* Cresson, Ariz. Fig. 162. *R. tabellaria* (Fitch), Mass. Fig. 163. *R. juniperina* Marcovitch, Mass. Fig. 164. *R. ebbettsi* n. sp. (holotype), Calif. Fig. 165. *R. persimilis* n. sp., B.C., Can. Fig. 166. *R. berberis* Curran, Ore. Fig. 167. *R. ribicola* Daane, Ore. Fig. 168. *R. cingulata* (Loew), Mass. (also typical of *indifferens*, *osmanthi* and *chiananthi*). Fig. 169. *R. basiala* (Osten Sacken), Mass. Fig. 170. *R. striatella* van der Wulp, Mexico. Fig. 171. *R. fausta* (Osten Sacken), N.H. Fig. 172. *R. cerasi* (Linn.), France.



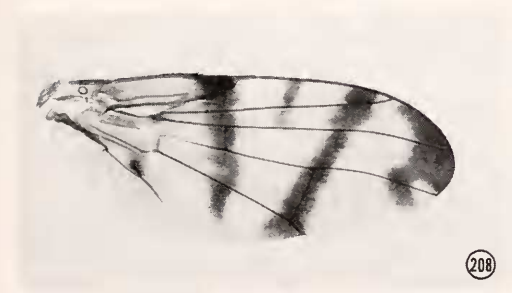
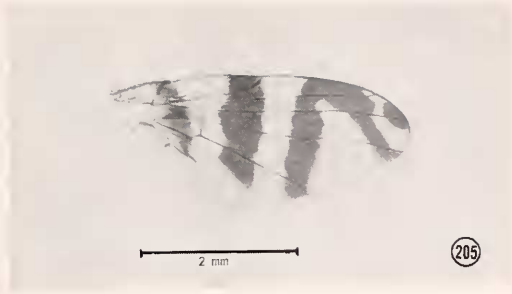
Figures 173-175. Postscutellum of *Rhagoletis* species. Fig. 173. *R. basiola* (Osten Sacken), ♂, Minn. Fig. 174. *R. basiola* (Osten Sacken), ♂, Minn. Fig. 175. *R. alternata* (Fallen), ♂, Germany. Figures 176-180. Anal cell of *Rhagoletis* species. Fig. 176. *R. ribicala* Doane, Ore. Fig. 177. *R. berberis* Curran, Ore. Fig. 178. *R. juniperina* Marcovitch, Mass. Fig. 179. *R. persimilis* n. sp., B.C., Can. Fig. 180. *R. tabellaria* (Fitch), Mass. Figure 181. Ventral receptacle of *R. cerasi* (Linn.), France. Figures 182-184. Ovipositor of *Rhagoletis* species. Fig. 182. *R. basiola* (Osten Sacken), Mass. Fig. 183. *R. pomonella* (Walsh), Mass. Fig. 184. *R. striatella* van der Wulp, Mexico.



Figures 185-194. Wing pattern of *Rhagoletis* species. Fig. 185. *R. pomonella* (Walsh), ♂, N.S., Can. Fig. 186. *R. pomonella* (Walsh), ♀, Mexico. Fig. 187. *R. zephyria* Snow, ♂, B.C., Can. Fig. 188. *R. mendax* Curran, ♀, Maine. Fig. 189. *R. cornivora* n. sp., ♀, Mass. Fig. 190. *R. suavis* (Loew), ♂, Kans. Fig. 191. *R. suavis* (Loew), ♀, Mich. Fig. 192. *R. completa* Cresson, ♀, Calif. (normal pattern). Fig. 193. *R. completa* Cresson, ♀, Calif. (abnormal pattern). Fig. 194. *R. baycei* Cresson, ♀, N.M.



Figures 195-204. Wing pattern of *Rhagoletis* species. Fig. 195. *R. juglandis* Cresson, ♀, Ariz. Fig. 196. *R. zoqui* n. sp., ♂, Hidalgo, Mex. Fig. 197. *R. tabellaria* (Fitch), ♂, Mass. Fig. 198. *R. juniperina* Marcovitch, ♀, Mass. Fig. 199. *R. persimilis* n. sp., ♀, B.C., Can. Fig. 200. *R. ebbettsi* n. sp., ♀ (holotype), Calif. Fig. 201. *R. ribicala* Doane, ♀, Ore. Fig. 202. *R. berberis* Curran, ♂, Ore. Fig. 203. *R. cingulata* (Loew), ♀, Fla. Fig. 204. *R. indifferens* Curran, ♂, Wash. (normal pattern).

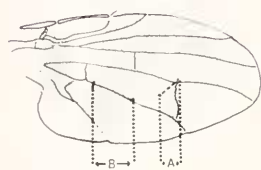


Figures 205–212. Wing pattern of *Rhagoletis* species. Fig. 205. *R. indifferens* Curran, ♂, Calif. (abnormal pattern). Fig. 206. *R. osmanthi* n. sp., ♀, Fla. Fig. 207. *R. chionanthi* n. sp., ♀, Fla. Fig. 208. *R. alternata* (Fallen), ♀, Germany. Fig. 209. *R. striatella* van der Wulp, ♀, Hidalgo, Mex. Fig. 210. *R. fausta* (Osten Sacken), ♀, N.H. Fig. 211. *R. cerasi* (Linn.), ♀, France. Fig. 212. *R. bosiala* (Osten Sacken), ♀, Mass.

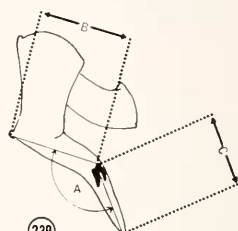
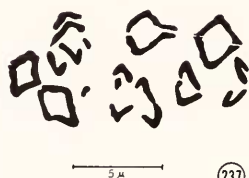


Figures 213-232. Chromosomes from anterior ganglia of larvae of *Rhagoletis* species. (Unless otherwise stated, sex unknown.) Fig. 213. *R. pomonella*, metaphase; ex *Pyrus Malus*, N.S., Can. Fig. 214. *R. pomonella*, anaphase; ex *Pyrus malus*, N.S., Can. Fig. 215. *R. zephyria*, late metaphase; ex *Symphoricarpos* sp., Ore. Fig. 216. *R. mendax*, metaphase; ex *Vaccinium* sp., N.H. Fig. 217. *R. cornivora*, ♂, metaphase; ex *Cornus amomum*, Mass. Fig. 218. *R. suavis*, metaphase; ex *Juglans cinerea*, Mass. Fig. 219. *R. suavis*, anaphase; ex *Juglans cinerea*, Mass. Fig. 220. *R. completa*, metaphase; ex *Juglans* sp., Calif. Fig. 221. *R. juglandis*, metaphase; ex *Juglans major*, Ariz. Fig. 222. *R. boycei*, metaphase; ex *Juglans major*, Ariz. Fig. 223. *R. zaqui*, metaphase; ex *Juglans mollis*, Hidalgo, Mex. Fig. 224. *R. cingulata*, metaphase; ex *Prunus serotina*, N.H. Fig. 225. *R. indifferens*, metaphase; ex *Prunus emarginata*, Calif. Fig. 226. *R. tabellaria*, metaphase; ex *Vaccinium* sp., Wash. Fig. 227. *R. juniperina*, metaphase; ex *Juniperus virginiana*, Mass. Fig. 228. *R. ribicola*, metaphase; ex *Ribes* sp., Ore. Fig. 229. *R. berberis*, ♀, metaphase; ex *Mahonia nervosa*, Ore. (SAT = satellite). Fig. 230. *R. berberis*, ♂, metaphase; ex *Mahonia nervosa*, Ore. Fig. 231. *R. basiala*, metaphase; ex *Rosa* sp., Mass. Fig. 232. *R. basiala*, anaphase; ex *Rosa* sp., Mass.

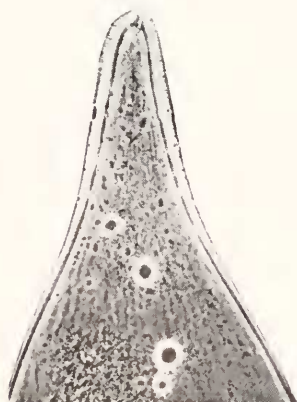




WING BAND RATIO = $\frac{A}{B}$



SURSTYLUS RATIO = $\frac{C}{B}$



Figures 233–237. Chromosomes from anterior ganglia of larvae of *Rhagoletis* species. (Unless otherwise stated, sex unknown.) Fig. 233. *R. basiola*, late prophase; ex *Rosa* sp., Mass. Fig. 234. *R. striatella*, metaphase; ex *Physalis* sp., Mexico, Mex. (SAT = satellite). Fig. 235. *R. striatella*, anaphase; ex *Physalis* sp., Mexico, Mex. Fig. 236. *R. fausta*, metaphase; ex *Prunus pennsylvanica*, Mass. Fig. 237. *R. fausta*, early anaphase; ex *Prunus pennsylvanica*, Mass. Fig. 238. Method for measuring wing band ratio in the *pomonella* species group. Fig. 239. Method for measuring surstylus ratio and angle in the *pomonella* species group. Fig. 240. Micropyle of egg of *R. striatella* van der Wulp. Fig. 241. Micropyle of egg of *R. pomonella* (Walsh).